WASH FLOW DISTURBANCE AND SUMMER WASH FLOW IN THE MOJAVE DESERT: INFLUENCE ON DISPERSION, PRODUCTION, AND PHYSIOLOGICAL FUNCTIONING OF DOMINANT SHRUBS

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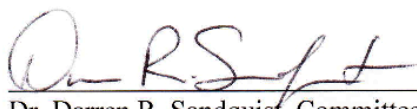of the Requirements for the Degree

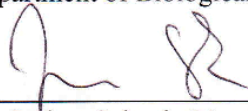Master of Science

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ABSTRACT

In many Mojave Desert ecosystems, water infiltrates to root-zones in greatest

proportion via washes. As such, washes have a pronounced effect on plant dispersion

and size across these landscapes. Desert roads alter the natural spatial patterns of washes

on alluvial fans (locally called bajadas) and potentially affect plant production and

distribution. As a winter-rainfall dominated ecosystem, climate changes in the Mojave

Desert that increase summer precipitation may also play an important role in altering

vegetation processes influenced by washes. Road effects on the spatial distribution of

desert plants on a Mojave Desert bajada were examined using remotely sensed LiDAR

data and ground based measurements of plant size. Plant physiological responses to

summer wash flow were also quantified by measuring gas exchange and water status of

two dominant perennial species, *Larrea tridentata* and *Ambrosia dumosa*. *Larrea* and

Ambrosia plants were nearly 7x and 4x larger where wash flow has been enhanced by

road culverts, relative to undisturbed areas and areas where flow has been cut-off by the

presence of a road/railroad. Clustering of large plants occurred along wash margins, with

clustering most pronounced in areas of enhanced wash flow. No clustering was found

where wash flow has been eliminated. For ecophysiological traits, both species showed

pronounced responses to the pulse of water; however, these responses varied as a

function of distance from wash. *Larrea* plants within 3 m and *Ambrosia* plants within ca.

2 m from the wash responded to the pulse of water. Leaf phenology dictated the timing

of carbon gain as *Larrea* experienced a rapid but short-lived increase in stomatal

conductance compared to a significant response for over a month following the pulse for

Ambrosia. These results indicate that disturbance of desert washes has a pronounced

impact on vegetation structure, and changing climatic conditions that impact plant

function could potentially lead to even greater vegetation shifts through time.

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CHAPTER 1

OVERVIEW

Water is the most important limiting resource in desert ecosystems (MacMahon
and Schimpf 1981; Noy-Meir 1973; Prentice and Werger 1985; Smith et al. 1997;
Woodell et al. 1969), and fluvial processes are primarily responsible for the creation of
desert land forms (Thornbury 1954). The Mojave Desert topography consists of
mountain ranges bordered by gentle sloping alluvial fans, which are created from water
and alluvium deposits from adjacent mountain runoff that extends out in a fan-like
fashion (Bedford et al. 2009; Thames and Evans 1981). Water flow across alluvial fans
generates a braided network of shallow stream channels (washes) that typically remain
dry, but flow following heavy rains (Thames and Evans 1981; Thornbury 1954). This
flow leads to a heterogeneous pattern of soil moisture (Bedford et al. 2009; Evans and
Thames 1981; Miller et al. 2009; Schlesinger et al. 1990), but these desert washes also
serve as catchment areas for runoff and promote rapid infiltration of water, which in turn
increases plant-available water across these networks (Heckman, Jr. and Berkas 1981;
Hillel and Tadmor 1962; McAuliffe 1995; Schwinning et al. 2011; Walter 1963). This
function makes washes an integral component of the hydrogeology of desert bajadas
(defined as a coalescence of alluvial fans), and because bajadas constitute up to 70% of
the total land surface in the Mojave Desert (Thornbury 1954), washes play a substantial
role in most ecological processes of this desert.

Water redistribution across desert bajadas is influenced by a wide variety of abiotic factors, including soil type, surface geomorphology, and the amount and timing of rainfall events. All of these factors have been shown to affect plant water availability and thus plant community structure and function (Miller et al. 2009; Tietjen et al. 2009). As such, disturbances on desert bajadas, such as roads that alter the natural water flow by changing the spatial patterns of desert washes, potentially affect plant production and distribution (Bolling and Walker 2000; Johnson et al. 1975; Lightfoot and Whitford 1991; Prose et al. 1987; Schlesinger and Jones 1984). Additionally, changes in climate and rainfall patterns, such as an increase in high-intensity summer storms and subsequent wash flow, may have a significant impact on the physiological functioning of desert plants, especially in the Mojave Desert where winter-rainfall is currently more dominate (MacMahon and Schimpf 1981; Smith et al. 1995).

The overall objectives of this study were to examine how the vegetation properties of a bajada in the Mojave National Preserve (MNP) are affected by disturbances that alter water input into the system. Water flow through washes has been disrupted due to a railroad and paralleling road bisecting a large desert bajada for the past 100+ years. The impact of this disturbance on plant dispersion and production was examined using remote sensing (airborne LiDAR). Additionally, an experimental manipulation (wash flow simulation) was performed to examine the impact of increased summer precipitation and subsequent runoff into washes on the physiological functioning of desert shrubs. This two-part study will present evidence of how climate and landscape changes may alter the relationships between washes and vegetation processes across a desert bajada.

CHAPTER 2

USE OF AIRBORNE LIDAR TO EVALUATE PLANT PROPERTIES IN THE
MOJAVE DESERT AND THE INFLUENCE OF WASH FLOW DISTURBANCE ON
THE DISPERSION AND PRODUCTION OF DOMINANT SHRUBS

Introduction

In desert ecosystems water is the resource that most limits plant productivity

(Pavlik 2008), and disturbances that influence the water availability to plants directly

affects the dispersion and production of desert shrubs (Bolling and Walker 2000; Johnson

et al. 1975; Prose et al. 1987; Schlesinger et al. 1990; Schlesinger and Jones 1984). The

spatial distribution of desert plants is directly linked to the pattern of available water, as

enhanced productivity has been observed along roadsides (Brooks and Lair 2009;

Johnson et al. 1975; Lightfoot and Whitford 1991) and wash margins (Balding and

Cunningham 1974; MacMahon and Schimpf 1981; Miller et al. 2009; Nimmo et al. 2009;

Prose et al. 1987; Schwinning et al. 2011). Plants growing along desert roadsides are

larger and more vigorous than non-roadside neighbors due to increased water availability

derived from surface runoff (Bolling and Walker 2000; Johnson et al. 1975; Lightfoot

and Whitford 1991). Despite this perceived benefit, roads are typically considered to be a

major disturbance in desert systems because of the direct effects of soil compaction,

alteration of soil structure, and destruction of long-lived desert perennials (Bolling and

Walker 2000; Prose et al. 1987). Indirectly, roads affect soil and vegetation properties by

altering the natural spatial pattern of desert washes, leading to wash flow diversion and

shifts in the pattern of plant available water (Schlesinger and Jones 1984; Schlesinger et al. 1989; Schwinning et al. 2011).

It is vital to understand the impact of disturbance on wash flow in desert ecosystems because ecological attributes such as growth, cover, and the spatial distribution of desert plants are largely influenced by the distribution of available water, which is often determined by the pattern and function of desert washes (Miller et al. 2009). Past studies of wash disturbance effects have been performed using conventional field sampling techniques such as transect and quadrat sampling (Prose et al. 1987; Schwinning et al. 2011; Schlesinger and Jones 1984); however, field sampling methods are time consuming and generally performed at small spatial scales. The large-scale spatial heterogeneity and complexity of desert landscapes, and subsequent trends of vegetation change along water-availability gradients, underscores the need for analyses at larger scales (MacMahon and Schimpf 1981; Miller et al. 2009). Various remote sensing technologies using satellite imagery and/or aerial photography have been used in arid environments to inventory and analyze vegetation characteristics at the landscape level (Frank and Tweddale 2006); but these methods provide little information about the microtopography of the landscape, which can dictate vegetation function and community structure (Rango et al. 2000). Airborne light detection and ranging (LiDAR) provides a means to examine such details across large landscapes.

Airborne LiDAR

Airborne LiDAR is a remote sensing technology that has the ability to examine the effects of microtopography on vegetation over large areas, thereby allowing quantification of larger-scale patterns. LiDAR data is collected from laser pulses emitted

by aircraft that reflect off of surfaces (leaves, branches, or ground) while concurrently recording the timing and intensity of the return pulse and the xyz location of laser points using a vector summation process (Habib et al. 2010). First and last return pulse data (point cloud) are representative of canopy height and ground, respectively. Products such as digital elevation models (DEM) and canopy height models (CHM) are created from the LiDAR point cloud, and are useful in characterizing vegetation properties across a landscape.

LiDAR has been used to measure tree heights in densely forested areas, where other methods (direct and indirect) are difficult to apply (Andersen et al. 2006; Brandtberg et al. 2003; Gaveau and Hill 2003; Hollaus et al. 2006; Wang and Glenn 2008). However, LiDAR-derived height measurements consistently underestimate actual tree heights, which must be accounted for using a correction factor determined by ground-truthing. Nonetheless, LiDAR-based forest surveys have been widely accepted due to the efficiency and cost effectiveness of obtaining vegetation characteristics over large areas (Andersen et al. 2006; Koukoulas & Blackburn 2005; Thomas et al. 2006; Wang & Glenn 2008). For forest canopies, LiDAR has proven to be a reliable estimate of canopy height, which is an important variable in assessing community structure such as plant (or stand) volume, growth and productivity (Lefsky et al. 2002; Wang and Glenn 2008).

Until recently, LiDAR has seldom been applied in arid ecosystems with relatively low-statured and sparse vegetation. The main limitation to using LiDAR in low-statured canopy systems is the problem of separating LiDAR returns, as vegetation returns are close to ground returns both spatially and temporally (Mitchell et al. 2011; Rango et al.

2000; Streutker and Glenn 2006). With the development of newer LiDAR systems that measure the intensity of returns and aid in the separation of multiple returns (Rango et al. 2000), the use of LiDAR-based surveys to obtain shrub heights in semi-arid systems has become increasingly popular (Hopkinson et al. 2005; Mitchell et al. 2011; Rango et al 2000; Sankey and Bond 2011; Streutker and Glenn 2006; Su and Bork 2007). However, as in forested systems, LiDAR consistently underestimates actual heights. For example, in sagebrush plant communities (Mitchell et al. 2011; Sankey and Bond 2011; Streutker and Glenn 2006) LiDAR underestimations of actual height ranged from 9% to 50%. Other studies have also shown that shrublands exhibit the greatest amount of error (underestimation) when compared to other taller vegetation classes (Hopkinson et al 2005; Su and Bork 2007). Fortunately, as in forest systems, a correction factor can be used to compensate for the error, but knowing the error is vital, as underestimation varies depending on the method employed to acquire LiDAR heights and the plant community type being studied. As such, field-based studies of LiDAR are needed to quantify the error and apply a unique correction factor for the ecosystem under examination.

Spatial Pattern of Desert Plants

LiDAR can also be used to evaluate spatial relationships among plants. Spatial relationships among desert plant communities have long been of interest to plant ecologists (MacMahon and Schimpf 1981; Pielou 1960; Prentice and Werger 1985; Woodell et al. 1969) in part because it is the first step to linking plant distributions with important ecological processes (Chou 1993). The dispersion pattern (non-randomness) of individual plants is measured in terms of spatial autocorrelation (SA), or the degree to which objects are related to other objects nearby (Chou 1993). Measurements of such

spatial relationships are important because, as explained by Tobler's first law of geography, "everything is related to everything else, but near things are more related than distant things." (Chou 1993). Positive SA exists when objects are aggregated or clustered; and conversely, negative SA refers to regularity, or uniform distributions (hereafter referred to as clustered and regular, respectively) (Galiano 1982; Perry et al. 2002). Random association is when no pattern exists and the objects exhibit spatial independence (Chou 1993; Pielou 1960).

Historically, desert shrubs have been described as regularly distributed (Barbour 1973), yet both regular and clustered patterns of dispersion have been observed in arid areas. Regular patterns of desert shrubs have been found to occur among large shrubs, and are most likely attributed to inter- and intra-specific competition for soil moisture (Phillips and MacMahon 1981; Prentice and Werger 1985; Schenk et al. 2003; Woodell et al. 1969). Woodell et al. (1969) found that regular patterns were prevalent in low rainfall areas and concluded that root competition for available water between neighboring plants facilitated the regular spacing of shrubs in the Mojave Desert. Such negative interactions have often been implicated as the cause of regularity within and between dominant Mojave Desert shrubs, but this interpretation assumes relatively uniform distribution of available water in the soil. An alternative explanation is that regular spatial patterns are dependent on abiotic factors, such as geologic substrate (Schenk et al. 2003). Furthermore, previous studies analyzing the spatial pattern of desert shrubs chose plots with a homogenous substrate, which is only achieved at very small spatial scales in desert regions (Fonteyn and Mahall 1981; Phillips and MacMahon 1981; Prentice and Werger 1985). Substrate homogeneity with uniform water distribution is

probably the exception in deserts, especially at larger spatial scales. Indeed, spatial heterogeneity of edaphic characteristics probably results in hydrologic heterogeneity across most desert landscapes (Bedford et al. 2009), rather than uniform water distribution. As such, regularity should be a rare occurrence in desert systems where surface runoff, accumulation and redistribution through a network of washes is common (Anderson 1971; Barbour 1973; Barbour and Diaz 1973; Phillips and MacMahon 1981; Woodell et al. 1969).

Others have argued that regularity may never be reached in arid areas due to frequent disturbances (e.g., flash floods, animal burrowing) that affect the growth and reproduction of interacting plants and subsequently lead to clustered patterns (Phillips and MacMahon 1981; Pielou 1960; Skarpe 1991). A number of studies have found that smaller and younger plants tend to be clustered due to vegetative regeneration or regeneration close to seed sources (Haase et al. 1996; Phillips and MacMahon 1981; Pielou 1960; Prentice and Werger 1985; Skarpe 1991). Clustering caused by such initial regeneration, followed by a transition towards regularity as these individuals grow larger, is a plausible outcome within homogeneous undisturbed environments. However, desert shrubs occupy habitat that is more typically heterogeneous and often disturbed, and their spatial distribution is strongly influenced by drivers of such processes, such as the presence of desert washes (Phillips and MacMahon 1981).

Many of these conflicting interpretations of spatial patterns come from ambiguities in field sampling methods, such as how to determine an individual vs. a clump of plants (Ebert and McMaster 1981). While airborne LiDAR does not make this distinction, it does provide a rigorous method of sampling that directly measures the

three-dimensional structure of plant canopies, facilitating the analysis of spatial patterns of plants over large areas. Using LiDAR, my study attempts to analyze the spatial pattern of Mojave Desert shrubs across a larger geographic extent, taking into consideration geomorphology, wash distribution and human disturbances as factors affecting plant spatial patterns.

Pattern Analysis. Spatial point pattern analyses in plant ecology are often used to determine the underlying processes causing the pattern. Two categories for spatial pattern analyses in plant ecology are global and local statistics. Global statistics, such as the Ripley's K-function ($K(d)$) (Ripley 1977) summarize the spatial pattern of the system as a whole, while local statistics such as the Getis-Ord statistic (G_i^*) (Getis and Ord 1992) reveal geographic pockets of clustering. When a global pattern is revealed across a study area, local statistics are used to show where on the landscape clustering or dispersion occurs, and can then be linked to other ecological attributes to explain the process that is driving the spatial distribution. Both of these statistics are second-order spatial statistics in that they describe the point pattern using all plant-to-plant distances, unlike first order statistics that use only nearest neighbor (Galiano 1982; Wiegand and Maloney 2004). This results in pattern detection across a range of scales, an important consideration as ecological processes are scale dependent (Galiano 1982; Wiegand and Maloney 2004).

Ripley's K-function has become a very popular tool for pattern analyses in plant ecological studies (Haase 1995; Haase et al. 1996; Koukoulas and Blackburn 2005; Prentice and Werger 1985; Skarpe 1991; Tirado and Pugnaire 2003); however, it is usually applied across small spatial scales (< 100 m) to satisfy the assumptions of stationarity (homogenous point pattern) and isotropy (uniformity in all orientations). A

homogeneous point pattern is one in which each point has an equal probability of occurring anywhere across the landscape and is independent of any other point, a situation that is not very common in natural ecosystems because the spatial structure of vegetation is strongly influenced by other biotic and abiotic factors (Law et al. 2009; Pelissier and Goreaud 2001; Wiegand and Moloney 2004). Assessing patterns over a large spatial scale using $K(d)$ requires that the entire study area be comprehensively sampled (Dixon 2002). This is very difficult and time consuming using conventional field methods. However, comprehensive sampling can be achieved relatively quickly and accurately using LiDAR systems. For example, LiDAR has been used in conjunction with Ripley's K-function to describe the spatial relationships between broad-leaved deciduous trees and gaps in a 80,000 m^2 plot of forested woodland in the United Kingdom (Koukoulas and Blackburn 2005).

While global methods have been widely used in describing point patterns in plant ecology, local methods may reveal pockets of spatial dependence that do not show up when using global statistics (Haase 1995; Perry et al. 2002). The G_i^* statistic is less sensitive to spatial non-stationarity within the data set (Getis and Ord 1992; Getis et al. 2003; Laffan 2006), and therefore can be a useful tool in analyzing point patterns in plant ecology, where spatial heterogeneity is commonplace. The G_i^* statistic uses a local sample, such as a neighborhood of defined size, and searches the nearby area for occurrences of more or fewer neighbors than expected in a random distribution. Significant high or low values are referred to as hotspots and coldspots, respectively (Getis and Ord 1992). Unlike global statistics, G_i^* identifies the location of clusters (hotspots) and can detect the distance over which that cluster persists (Ord and Getis

1995; Perry et al. 2002; Sokal et al. 1998). The G_i^* statistic has often been used in socio-political and health-related research such as epidemiological studies for the detection of disease hotspots and an assessment of the disease spread (Getis et al. 2003; Ord and Getis 1995). In contrast, G_i^* has rarely been applied in plant ecological studies, although Laffan (2006) used G_i^* to assess the spatial distribution of weed infestations and to prioritize management efforts for the control of infestation at the regional scale (Laffan 2006).

Experimental Goals

The overall objective of this study is to examine the effect of wash flow disturbance on the size and spatial distribution of Mojave Desert shrubs. My specific aims are to demonstrate the ecological applicability of LiDAR in this desert system and then use LiDAR-measured plant heights to characterize vegetation properties and their relationships to wash disturbance across a large Mojave Desert landscape. The study area investigated is a bajada bisected by a railroad and paralleling paved road (hereafter referred to collectively as the "road"). The road represents a > 100-year old disturbance since the railroad was installed in 1905. The area upslope from the road exhibits uninterrupted water movement and natural channel patterns across the bajada. The road disrupts downslope water flow by funneling runoff into culverts passing under the railroad, resulting in altered channel patterns below the road. Where outflow occurs below the road large "superwashes" have been created due to enhanced wash flow. Alternatively, water input is significantly reduced in areas between superwashes where natural channel flow originating upslope is no longer received (Fig. 1).
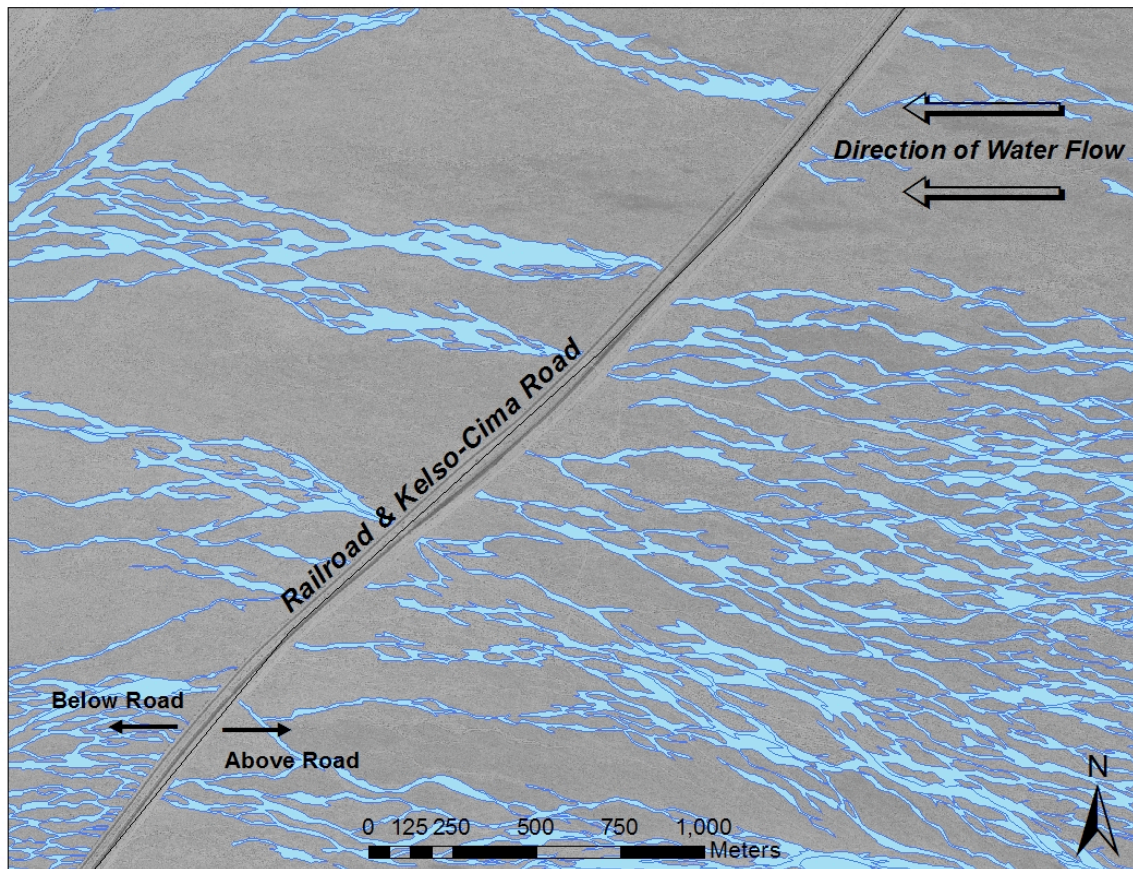
Figure 1. Digital orthophoto quadrangle (DOQ) of the Hayden piedmont, located within the Mojave National Preserve, in the Mojave Desert, CA, USA. Surficial geologic maps (Miller et al. 2009) show active alluvial fan channels (Qaa, light blue) above (to right) and below (to left) a railroad and paralleling paved Kelso-Cima Road after 100 years of wash flow disturbance. Active washes were determined using the classification system described by Bedford et al. (2006) where Qaa represents active alluvial fan channels that have dominant wash sediment present, even if older soil is present underneath the young deposits. Above Road wash flow has been unaffected by the road disturbance, while Below Road wash flow has either been enhanced or reduced due to the diversion of water into culverts under the railroad.

To determine if LiDAR can accurately predict plant height and if there is a minimum size threshold for LiDAR detection, I quantified the relationship between field-measured plant heights and LiDAR-derived plant heights (i.e., LiDAR validation). I hypothesized that there would be a linear relationship between field measured plant heights (H_{Field}) and LiDAR-determined plant heights (H_{LiDAR}) and that some degree of correction would be necessary because LiDAR has been shown to consistently

underestimate actual plant heights in the few arid ecosystems previously studied
(Hopkinson et al. 2005; Mitchell et al. 2011; Sankey and Bond 2011; Streutker and Glenn
2006; Su and Bork 2007).

Secondly, I used global and local methods of spatial autocorrelation from LiDAR-
derived plant heights to assess how the influence of disturbed surface hydrology has
impacted the spatial distribution of long-lived desert shrubs across a large desert bajada.
I hypothesized that clustering would be present in both disturbed (below road) and
undisturbed (above road) areas due to wash flow alterations (Schlesinger and Jones 1984;
Skarpe 1991) and environmental heterogeneity (Law et al. 2009; Pelissier and Goreaud
2001). However, I predicted that spatial clustering would be strongest below the road, as
indicated by a more rapid increase in $K(d)$ vs. distance (O'Sullivan and Unwin 2003).
Local spatial patterns were evaluated within predefined study plots (See Methods) across
the desert bajada. Because of the relationship between plant growth and water
availability, clustered patterns of vegetation were predicted to occur in water enhanced
areas and adjacent to active washes, but be absent where wash flow has been cut off
(Schlesinger and Jones 1984; Woodell et al. 1969)

Finally, the effect of wash flow disturbance on plant productivity was quantified
in terms of plant height (m) and volume (m^3) as determined by field measurements that
were used to validate the accuracy of LiDAR. Plant size and volume was predicted to be
greatest in areas where wash flow has been artificially increased, and lowest in areas
where wash flow has been cut off (Balding and Cunningham 1974; Johnson et al. 1975;
Schlesinger and Jones 1984; Schwinning et al. 2011).

Methods

Study Area

The study area was located at the Hayden piedmont (or bajada[1]) within the
Mojave National Preserve (35°02'N, 115°36'W), approximately 50 km SE of Baker, CA
and 5 km NE of the Kelso train depot. The Hayden piedmont is at the Northern foot of
the Providence Mountains and is bisected by the Kelso-Cima Road and paralleling
railroad (hereafter referred to as "road") (Fig. 1). Within the study area the terrain is a
gentle sloping alluvial fan, elevations ranging from 715 to 845 m across ca. 3.3 km, with
numerous shallow washes occurring across the bajada. The vegetation in the study area
is dominated by the perennial shrubs *Larrea tridentata* (creosote bush) and *Ambrosia
dumosa* (white bursage) (hereafter referred to as *Larrea* and *Ambrosia)*. *Larrea* is an
evergreen shrub that reaches heights > 2 m at maturity, whereas *Ambrosia* is a drought
deciduous shrub that rarely exceeds 1 m in height (Hamerlynck et al. 2002; Schenk et al.
2003). The *Larrea-Ambrosia* desert scrub vegetation type occupies approximately 70%
of the total area of the Mojave Desert (Evans & Thames 1981). Soil maps, usually
available from the USDA Natural Resources Conservation Service (NRCS), are not
available for this area; however, surficial geologic maps for the study area have been
provided by the USGS, Menlo Park, CA, USA (Miller et al. 2009) which characterize soil
horizon properties and geomorphology (Bedford et al. 2009). These maps of the Hayden
site show how the presence of a railroad and paralleling road bisecting the bajada for over
100 years has altered surface hydrology, including washes (Fig. 1). Visual inspection of

[1] A bajada is a term typically used for a piedmont in the desert, and both refer to a coalescence of adjacent
mountain-front alluvial fans (Peterson 1981; Thornbury 1969). Except when referring formally to the
Hayden piedmont, the term bajada will be used herein to represent this land-form.

LiDAR imagery for the site (described below) and vegetation patterns led to the creation of three study units (with 2 plots in each): Above Rd = areas with undisturbed ephemeral stream channel flow, upslope from road; Below Rd + = areas below the road with enhanced wash flow due to diversion by the road; and Below Rd - = areas below the road, with deprived wash flow due to flow diversion by the road (Fig. 2).
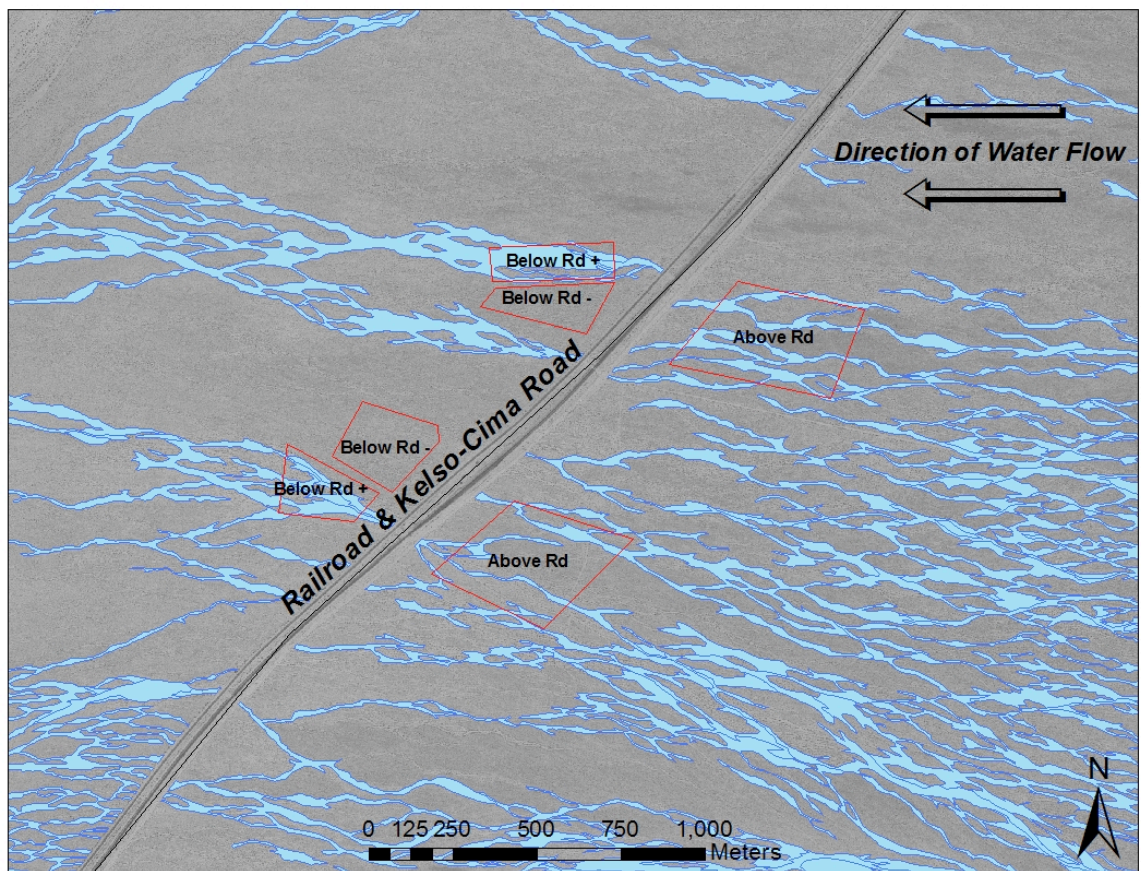
Figure 2. Location of six study plots in relation to dominant active washes. Above Rd plots are in an area with undisturbed wash flow. Below Rd + are where water has been artificially enhanced due to the diversion of water by the road. Below Rd - are where wash flow has been cutoff due to diversion.

Data Acquisition and Processing

The LiDAR data were acquired on October 5, 2004 by Airborne 1 Corporation (El Segundo, CA), and processed by the USGS (Jonathan Stock, Menlo Park, CA). Data included first and last return point cloud data (.las binary format) containing 3-dimensional spatial coordinates (xyz), and two DEM's of 1 m resolution consisting of a "first return" digital surface model (DSM) that includes vegetation, and a "bare earth" DEM with vegetation removed, or digital terrain model (DTM). The bare-earth surface was generated by filtering the last return pulse data using TerraSolid Software's TerraScan® program (Stock et al. 2008). The points were kriged using Golden Software's Surfer® with linear averaging over 10 m, resulting in a 1 m resolution DTM (Stock et al. 2008). A canopy height model (CHM) was created by subtracting the DTM from the DSM, resulting in a LiDAR-determined vegetation height value associated with every 1 m grid cell.

First and last return .las files consisted of over 21 million individual points, covering ~1,839 ha, with an average point spacing of 0.92 m. The average point density was 4.48 points / m^2 with varying local point densities ranging from 0.25 to 29 points / m^2; 60% of which contained greater than 4 points / m^2. By convention, a high point density is anything greater than 4 points / m^2 with sampling densities varying from 0.6 to 24 points / m^2 reported in forest studies (Andersen et al. 2006).

LiDAR Accuracy. Point cloud data, when compared to GPS data collected for control points, resulted in 0.4 m vertical accuracies and 0.1 m horizontal accuracies (Jonathon Stock pers. comm.). When the point cloud data was processed into the bare-earth DEM, local linear streaking patterns were observed (Stock et al. 2008). These

patterns appear to be an artifact in the data due to flight overlap. Typical flightline overlap is 10-20% (training.ESRI.com) but has been reported up to 50% (Streutker and Glenn 2006). The overlap of multiple flightlines can result in poor relative vertical accuracies of 25 cm or more and can be corrected by separately analyzing the individual flightlines using the GPS timestamp from the raw point could data (Streutker and Glenn 2006; Nancy Glenn pers. comm.). The .las files obtained from Airborne 1 did not contain the GPS timestamp so separation of individual flightlines was not possible for this analysis. The artifacts in the bare-earth DEM may have also been associated with possible scale errors from swaths with systematically different elevations (Stock et al. 2008). Fixes to these artifacts have not been found and therefore, the dataset used has an uncertain amount of error. To reduce the amount of error in this study, we carefully selected our study sites to avoid these streaking patterns.

Validation Study

Field Data Collection. In order to assess how accurately LiDAR predicts actual field heights of vegetation, ground-based validation surveys were conducted in January 2009 and January 2010. A total of 448 (n = 132 and n = 316 for 2009 and 2010, respectively) ground-based vegetation validation points were obtained with manual measurements of the following attributes: species, number of plants (when point included more than one plant), maximum plant height, maximum plant length, and plant length perpendicular to maximum. Validation points were all collected within the three study units (six plots total) described above.

In 2009, validation points were chosen by navigating to plants 1-4 m tall, as determined by the CHM, using Trimble Juno ST global positioning system (GPS)

receivers (Trimble Navigation, Sunnyvale, CA, USA). Due to GPS inaccuracies it was sometimes difficult locating points in the field that corresponded to the LiDAR-determined 1-4 m tall plant, so we took a different approach the following year. In 2010, validation points were chosen by sampling all plants within 30 x 10 m subplots (2 subplots per study unit) and recording the same attributes as those in 2009, plus one additional height measurement; an average height calculated from height measurements taken at four corners of a one meter square centered on top of the plant.

Field Height vs. LiDAR Height. Due to horizontal inaccuracies associated with using non-differentially corrected GPS units for field data collection, the exact GPS locations of field data in relation to the raw point data cloud locations were uncertain. Therefore, the grid-based CHM was used to compare LiDAR heights with field heights by applying a spatial buffer. The 1-m resolution CHM was converted to a point file in which a point was centered in each 1 m^2 grid cell with the LiDAR determined height for that cell. A spatial buffer of 2 m was applied to all field points and the maximum LiDAR height within the 2 m buffered zone was selected as the LiDAR height to compare with the field-measured height. The spatial buffer allows for GPS horizontal inaccuracies and 1.5 m has been shown to have the highest correlation between field-measured heights and LiDAR-calculated heights in other low canopy systems (Streutker and Glenn 2006). A 2 m buffer was chosen to ensure that the buffer captured values of grid cells within a 1.5 m radius.

Data Analysis. All data analyses were performed using SAS for Windows (Version 9.0, SAS Institute Inc., Cary, NC, USA). For the validation study, a number of regression analyses were performed to determine the accuracy of LiDAR-measured plant

heights (dependent variable) using field measured plant heights (explanatory variable).

Simple linear regression (SLR) is described by the equation:

$$Y = \beta_0 + \beta_1 X \qquad \text{(Eq. 1)}$$

where β_0 is the y-intercept, β_1 is the slope (also called the regression coefficient), X is the value of the independent variable (field-measured plant height, H_{Field}), and Y is the value of the dependent variable (LiDAR-measured plant height, H_{LiDAR}). Before SLR can be used to test research hypotheses, the following assumptions about the distribution of Y must be met: linearity, equal variances, independence, and normality. Checking for normality and equal variances can only be done with histograms and/or probability plots and residual plots, respectively, which require that the SLR is conducted initially. Normality was assessed using the Kolmogorov-Smirnov, Cramer-von Mises, and the Anderson-Darling goodness-of-fit tests for normal distribution generated by SAS. Linearity was checked through visual analysis of the relationship of X vs. Y on a scatterplot, and a random pattern around zero in the residual plot. When all assumptions have been met, SLR can then be used to test the null hypothesis (H_0) that the slope of the regression line equals zero ($H_0: \beta_1 = 0$), or the alternative hypothesis (H_a) that the slope does not equal zero ($H_a: \beta_1 \neq 0$). If a significant linear relationship is present (H_0 rejected), the regression $H_{LiDAR} = \beta_0 + \beta_1 H_{Field}$ provides a valid model that, when rearranged to $H_{est} = (H_{LiDAR} * \beta_1) + \beta 0$ can be used to estimate plant heights (H_{est}) from LiDAR data.

Spatial Analysis

To examine spatial patterns and clustering of large plants, the CHM was converted into a point shapefile and then classified into plant size classes based on

individual LiDAR points 1-4 m tall. Points within 100 m of the road or railroad were

excluded to eliminate error from edge effects, and data was analyzed separately for above

road (undisturbed wash flow) and below road (disturbed wash flow) (Fig. 3). Global and

local clustering were analyzed using all data points shown in Figure 3 and spatial patterns

were quantified in relation to the three study units (Above Rd, Below Rd +, Below Rd -)

and surficial geologic map.

  <u>Analysis of Global Spatial Patterns using Ripley's K-function</u>. The analysis of

spatial homogeneity (global spatial patterns) was done using Ripley's K-function (Ripley

1977), the most widely used global statistic for point pattern analysis in ecological studies

(Perry et al. 2002). Visual analysis of 1-4 m plants both above and below the road

revealed non-random patterns (Fig. 3), warranting further investigation to confirm the

existence of plant patterns across varying spatial scales. While a homogeneous substrate

is generally a prerequisite for studying spacing patterns using global clustering methods

(Phillips and MacMahon 1981; Skarpe 1991), homogeneity is hard to achieve in desert

regions where runoff channels or washes are commonplace (Anderson 1971; Barbour and

Diaz 1973). Within the study area, spatial heterogeneity and anisotropy (directional

dependence) does exist because plants are more
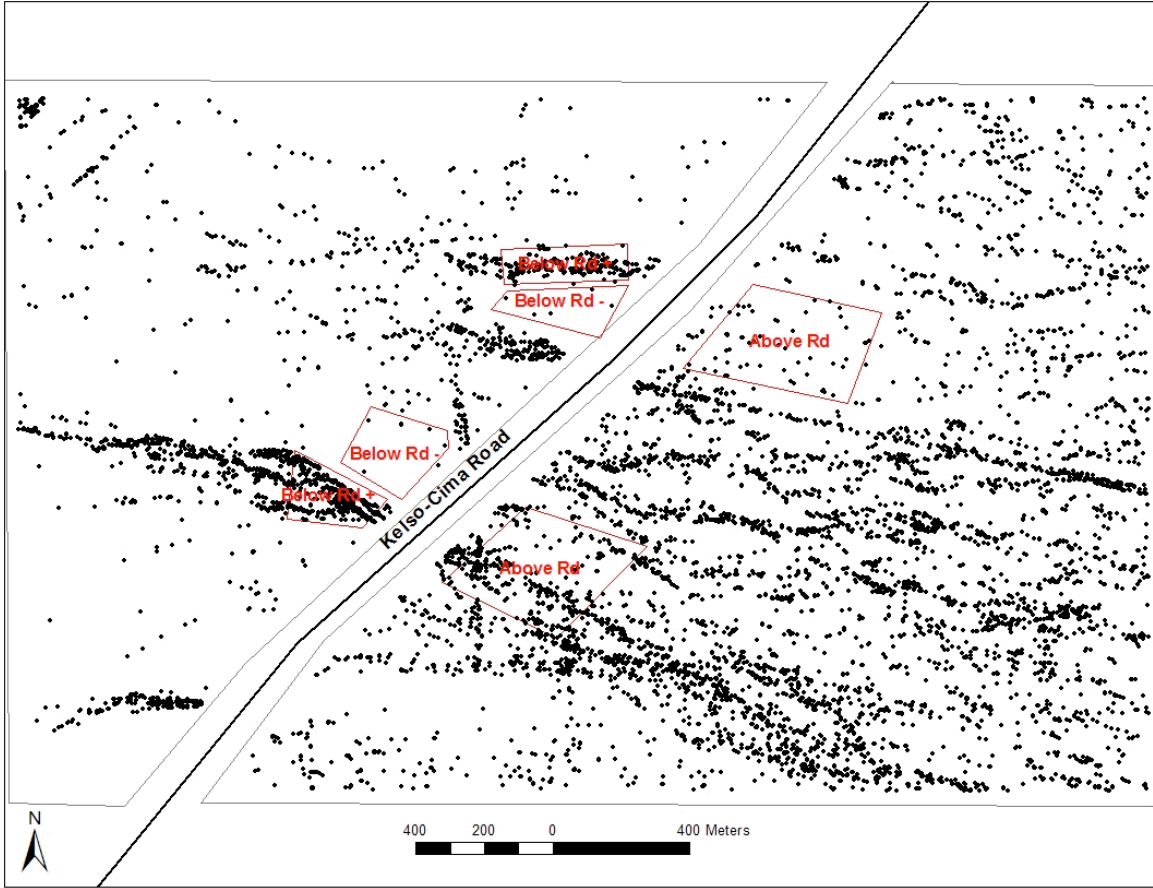
Figure 3. LiDAR-determined plants classified as 1-4 m tall across the Hayden study area. Black dots represent all 1-4 m vegetation points. Points within 100 m of the road were excluded to avoid edge effects. Global and local clustering evaluations were done separately for above road and below road areas.

likely to survive along wash margins where water availability is the greatest.

Nevertheless, because $K(d)$ is defined in terms of randomly chosen events (i.e., plants

could theoretically occur anywhere across the full scale of the site), global patterns are

still interpretable for non-homogeneous point processes (Dixon 2002).

Ripley's K-function evaluates the observed spatial pattern of plants and compares

it to one expected by a homogenous Poisson point process. The K-function considers

each point (i) (in this context, points represent plants) the center of a circle of radius d,

and counts the numbers of neighbors (j) within that circle. Under the null hypothesis of

complete spatial randomness (CSR), $K(d) = \pi d^2$ (i.e., the area of a circle of radius d)

for all d, and when plotted, $\sqrt{K(d)}$ vs. d will be linear and represent the expected random

point process. If the observed number of plants within a given distance d of each i is

greater than that expected for a random distribution, the distribution is more clustered

than a random distribution at that distance, and the observed line will fall above the

expected $\sqrt{K(d)}$ vs. d line. On the other hand, if the observed number of plants within a

given distance d of each i is smaller than that expected for a random pattern, the

distribution is more dispersed than random, and the observed line will fall below the

expected line. For statistical significance, a test from departure of complete spatial

randomness was applied using confidence envelopes for $K(d)$ by randomly re-distributing

the points in the study area using 999 Monte Carlo permutations (99.9% confidence

envelope). If the observed K value is larger than the upper confidence envelope, spatial

clustering is significant at that distance. Where K is smaller than the lower confidence

envelope, significant regularity occurs at that distance. Where the observed K values fall

within the bounds of the confidence envelope, the null hypothesis of complete spatial

randomness cannot be rejected.

Ripley's K-function was analyzed using ArcGIS 10.0 which uses a common

transformation of the original K-function, $L(d)$. $L(d)$ is calculated as:

$$L(d) = \sqrt{\frac{A \sum_{i=1}^{n} \sum_{j=1, j \neq 1}^{n} k\,(i,j)}{\pi n (n-1)}} \qquad \text{(Eq. 2)}$$

where n is equal to the total number of features (plants), A represents the total area of the

features, $k_{i,j}$ is a weighting term that is used to correct for boundary effects of the study

plot, and d is distance, or radius of the circle centered on each plant. The boundary

correction used in ArcGIS 10.0 was the "simulate outer boundary values" method. This approach uses edge points to create replicate points across the study area boundaries, to provide a more accurate neighbor estimate near the area boundaries. These points are used only for edge correction and are not used in the K-function calculation. Prior to plotting $L(d)$, lower, and upper confidence envelopes were transformed by subtracting d which sets the expected value of $L(d)$ to zero when the pattern is Poisson-random. Plotting $L(d) - d$ vs. d has become common practice when reporting K-function results and facilitates easier interpretation of spatial patterns across all interpoint distances (Pelissier and Goreaud 2001).

Local Clustering and the Getis Ord (G_i^*) Statistic. The local statistic, Getis Ord (G_i^*), further allowed the identification of where, across the study area, clusters occurred, the critical distance at which plant clustering ceased, and how clustering compared across patterns of disturbance. Local measures of SA use group-level data or aggregated data, as opposed to individual level data used with global statistics. This requires defining geographic units to characterize spatial patterns. For this study, a grid of 20 x 20 m was overlaid onto the LiDAR map to represent a neighborhood of plants. This is the same plot size used by Schenk et al. (2003) to assess the spatial pattern of *Ambrosia* relative to other *Ambrosia* and *Larrea* plants in the Mojave Desert.

Frequency values were determined for each grid (hereafter referred to as a neighborhood) that represents the number of 1-4 m LiDAR points (plants) that fell within that neighborhood. For G_i^* the neighborhood of interest, i, is compared to neighbors at distance d from i, looking for occurrences of more or fewer plants than expected based on the mean of the whole dataset (Getis and Ord 1992; Laffan 2006; Ord and Getis 1995).

Local clustering was analyzed at distances of 10 m, which includes only the neighborhood of interest, and over 50 and 100 m, which includes adjacent neighborhoods.

The G_i^* statistic was calculated using the hotspot analysis tool in ArcGIS 10.0. G_i^* is calculated as:

$$G_i^*(d) = \frac{\sum_j w_{ij}(d)x_j - W_i^* \bar{x}^*}{s^* \sqrt{\frac{(nS_{1i}^*) - W_i^{*2}}{n-1}}} \qquad \text{(Eq. 3)}$$

where i is the neighborhood of analysis (center of local sample), j is the neighboring samples, d is the lag or clustering distance (10, 50 or 100 m in this study), w_{ij} is the weight for neighbor j from location i, n is the number of samples in the dataset, W_i^* is the sum of weights, S_{1i}^* is the number of samples within d of the central location, $\bar{x}^*$ is the mean number of plants per neighborhood across the whole unit of study, and s^* is the standard deviation of the mean number of plants per neighborhood. The weights matrix $\sum_j w_{ij} (d) x_j$ represents the sum of all the plants that fall within the distance (d) from i to j.

The output scores from the G_i^* analyses are z-scores, which gives the relative position of a value along a normal distribution and describes how the data are distributed around the mean. Positive values represent clusters that are greater than the mean and negative values represent clusters that are less than the mean. For this study, a G_i^* score threshold of +2.57 was chosen to represent significant clustering (hotspots) of large plants, corresponding to a 99% confidence interval and a p-value of 0.01. Based on this criterion, each neighborhood was assessed for clustering and if the G_i^* score was ≥ 2.57 at 10 m, strong clustering of plants occurred within that neighborhood. When clustering continues to neighbors within 50 m of i, the G_i^* score will be higher at 50 m than at 10 m,

and likewise for 100 m. If the G_i^* score does not increase with distance, then the clustering no longer exists at the greater distance, thus the highest G_i^* score is the critical distance at which clustering (hotspots) occur.

The resultant map of the critical distances at which clustering occurred facilitated the comparison of the effects of wash flow and disturbance on vegetation among the three study units. This map can be used in conjunction with the surficial geology map to determine the footprint that active washes of varying size have on surrounding vegetation. Additionally, this type of analysis, from remotely sensed data of plants, could be used to determine the location of active washes and provide information on surface hydrology, which can ultimately aid in predictive modeling.

Plant Size

The mean maximum plant height (m) and mean volume of individual plants (m^3) for *Larrea* and *Ambrosia* were compared among the three study units using the ground based measurements that were taken to validate LiDAR. Plant volume (m^3) was calculated for *Larrea* as the volume of an inverted cone ($1/3 \pi r^2 h$; where $r^2 = 1/2$ length * $1/2$ width, i.e., max length and length perpendicular to max length, respectively) (Hamerlynck et al. 2002; Franco et al. 1994; Schlesinger and Jones 1984); and for *Ambrosia* as a hemisphere ($2/3 \pi r^3$; where $r^3 = h$ * $1/2$ length * $1/2$ width) (Hamerlynck et al. 2002; Schlesinger and Jones 1984). To satisfy the assumptions of ANOVA the data must be independent, normal and have equal variances. SAS tests for normality included Shapiro-Wilk, Kolmogorov-Smirnov, Cramer-von Mises, and Anderson-Darling.

Plant heights were found to have a non-normal distribution for *Larrea* Below Rd -, and *Ambrosia* Below Rd + and Below Rd - (all tests $p < 0.05$). Boxplots revealed

that there were potential outliers in the datasets but the values themselves were not

unreasonable (not errors in sampling) and were not taken out of the dataset. The main

obstacle to using ANOVA for these datasets was the unbalanced sample size, which

caused violation of the assumption of equal variances. Therefore, a non-parametric

Kruskal-Wallis (KW) test was used. Multiple comparisons were made by applying the

Bonferroni correction to the alpha level (0.05/3 = 0.0167) and then running multiple

pairwise Wilcoxon tests.

For plant volume, the assumptions of normality (all tests p < 0.05) and equal

variances (due to unequal sample size) were violated. Therefore, the KW test was used

to compare mean plant volume (m^3) among the three study units, and multiple pairwise

Wilcoxon tests were run post-hoc (alpha level = 0.0167 after Bonferroni correction) to

test for differences between study unit pairs.

<div align="center">Results</div>

Validation Study

There were a total of 448 plants measured in the field that were used to test

LiDAR as an accurate predictor of plant height: 141 *Larrea*, 211 *Ambrosia*, 2 *Cholla*

spp., 2 *Yucca spp.*, 80 mixed (e.g., *Ambrosia* growing under a *Larrea* plant), and 12

classified as other (unknown by the observer). When all plants were considered, H_{LiDAR}

was significantly correlated with H_{Field} ($R^2 = 0.58$ $P < 0.0001$) (Table 1, Fig. 4).

However, for *Ambrosia* LiDAR height was not correlated with field height when

analyzed alone, ($R^2 = 0.0008$; $P = 0.68$) (Table 1, Fig. 5). The non-linear pattern

exhibited by *Ambrosia* indicated that LiDAR may not be effective in predicting heights

of smaller-statured plants. This was further illustrated by the lack of a random

distribution around zero, up to approx. 0.3 m, and the larger spread of residuals at smaller H_{LiDAR} values in the plot of residuals vs. predicted values of H_{LiDAR} (Fig. 6).

Exclusion of *Ambrosia* (n = 237) from subsequent analyses revealed H_{LiDAR} as a reliable estimate of H_{Field} for all remaining plants ($R^2 = 0.58$ $P < 0.0001$) (Table 1, Fig. 7). The significance value did not change from the analysis including *Ambrosia*, but a different regression equation resulted (Table 1). The residual plot revealed that the majority of the remaining points displayed a random distribution around zero, yet there was still an aggregation of residual points for H_{LiDAR} values less than approx. 0.3 m, suggesting minor biases in the regression owing to small plant sizes (Fig. 8).

Table 1. Simple linear regression (SLR) results for validation study of LiDAR-determined plant heights.

	Regression Model	Correlation Coefficient & Model Significance
Maximum Height		
All Samples (n = 448)	$H_{est} = (H_{LiDAR} \times 0.50) - 0.11$	$R^2 = 0.58$; $P < 0.0001$
Ambrosia dumosa only n = 211)	$H_{est} = (H_{LiDAR} \times 0.07) + 0.13$	$R^2 = 0.0008$; $P = 0.68$
Ambrosia dumosa excluded (n = 237)	$H_{est} = (H_{LiDAR} \times 0.65) - 0.43$	$R^2 = 0.58$; $P < 0.0001$
Single Plants* (n = 89)	$H_{est} = (H_{LiDAR} \times 0.66) - 0.46$	$R^2 = 0.62$; $P < 0.0001$
Average Height		
All Samples* (n = 114)	$H_{est} = (H_{LiDAR} \times 0.50) - 0.22$	$R^2 = 0.27$; $P < 0.0001$
Single Plants* (n = 42)	$H_{est} = (H_{LiDAR} \times 0.65) - 0.40$	$R^2 = 0.48$; $P < 0.0001$

Note: H_{est}: estimated plant heights from LiDAR data, H_{LiDAR}: LiDAR determined plant heights. * indicates that *Ambrosia dumosa* has been excluded from the model.

   The 0.3 m cutoff in the residual plot was used to suggest a minimum size
threshold for acceptable LiDAR accuracy. Two lines of evidence support the 0.3 m
threshold. First is the apparent lack of correlation between H_{LiDAR} and H_{Field} below
approx. 0.3 m (Figs. 4 and 7). Second, is that with *Ambrosia* excluded, no field samples
were smaller than 0.29 m height. When H_{LiDAR} points less than 0.3 m were removed from
the SLR analysis, the residual plot showed a more clearly random pattern (Fig. 9).
LiDAR's ability to accurately measure plant height below 0.3 m in this study appears to
be unreliable, thus 0.3 m was determined to be the lower limit for LiDAR detection in
this desert system.
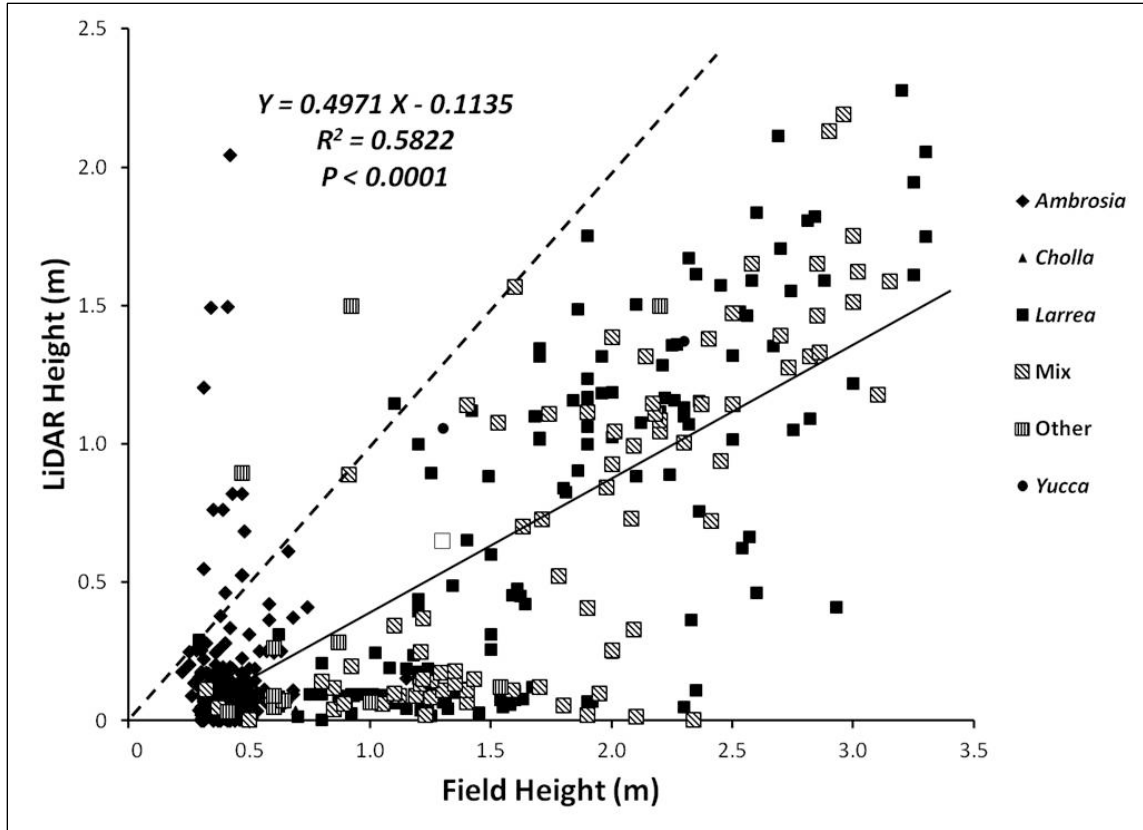
Figure 4. Simple Linear Regression of field-measured maximum heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) for all plants (n = 448) coded by species. The solid line represents the best fit linear regression line, while the dashed line represents the 1:1 correspondence. There is a significant linear relationship ($P < 0.0001$) between H_{Field} and H_{LiDAR} explaining 58% of the variation in Y.

To determine if average height, rather than maximum height, was better correlated with LiDAR heights, a regression was run using only those plants that had an average height measured (n = 114). A significant relationship still existed between H_{LiDAR} and H_{Field} ($P < 0.0001$), but the predictive value of H_{LiDAR} was much weaker ($R^2 = 0.27$) (Table 1, Fig. 10). Estimations of plant height from LiDAR data were consistently underestimated whether using field-measured maximum height (excluding *Ambrosia*) versus H_{LiDAR} (mean error = -1.04 m; RMSE = 0.40 m), or field-measured average height versus H_{LiDAR} (mean error = -0.71; RMSE = 0.34 m).
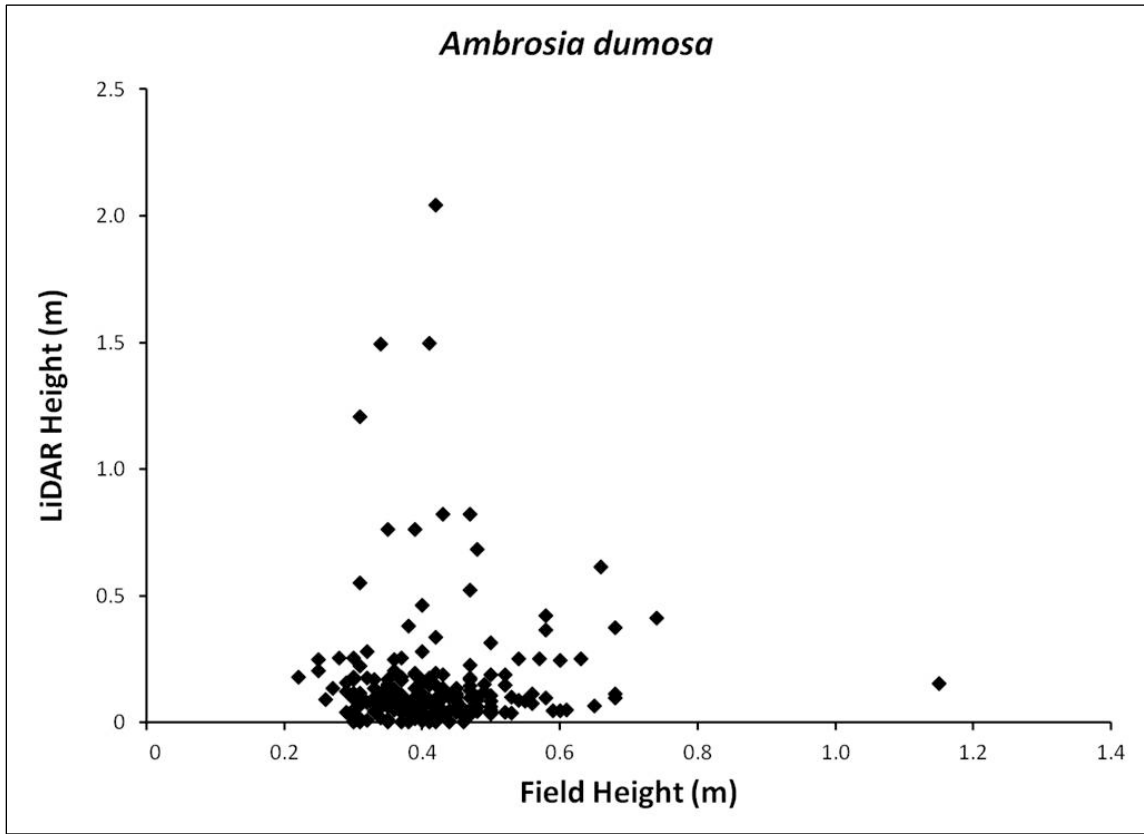
Figure 5. Simple Linear Regression of field-measured maximum heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) for *Ambrosia dumosa* alone (n = 211). There is no significant relationship (*P* = 0.68).

An analysis consisting of only single plants (n = 89) was performed based on the findings of Streutker and Glenn (2006) who determined that a 1.5 m buffer was optimum for capturing isolated sagebrush shrubs, and subsequently increased their R^2 value from 0.64 (when all validation points were included) to 0.72. Similarly, I found that field-measured maximum height of single *Larrea* plants, which constituted 97% of the sample, were slightly better correlated with LiDAR-determined plant heights ($R^2 = 0.62$; *P* < 0.0001) than for any other sample combination (Table 1, Fig. 11). H_{LiDAR} was also better correlated with field-measured average height of single *Larrea* plants (n = 42) ($R^2 = 0.48$, *P* < 0.0001) when compared to average heights that included clumps of more than one

plant (Table 1, Fig. 12). Underestimations of height for single *Larrea* plants were very

similar to those obtained when clumps of plants were included in the analysis for both

maximum height (mean error = -1.03 m; RMSE = 0.38 m) and average height (mean

error = -0.75 m; RMSE = 0.29 m).
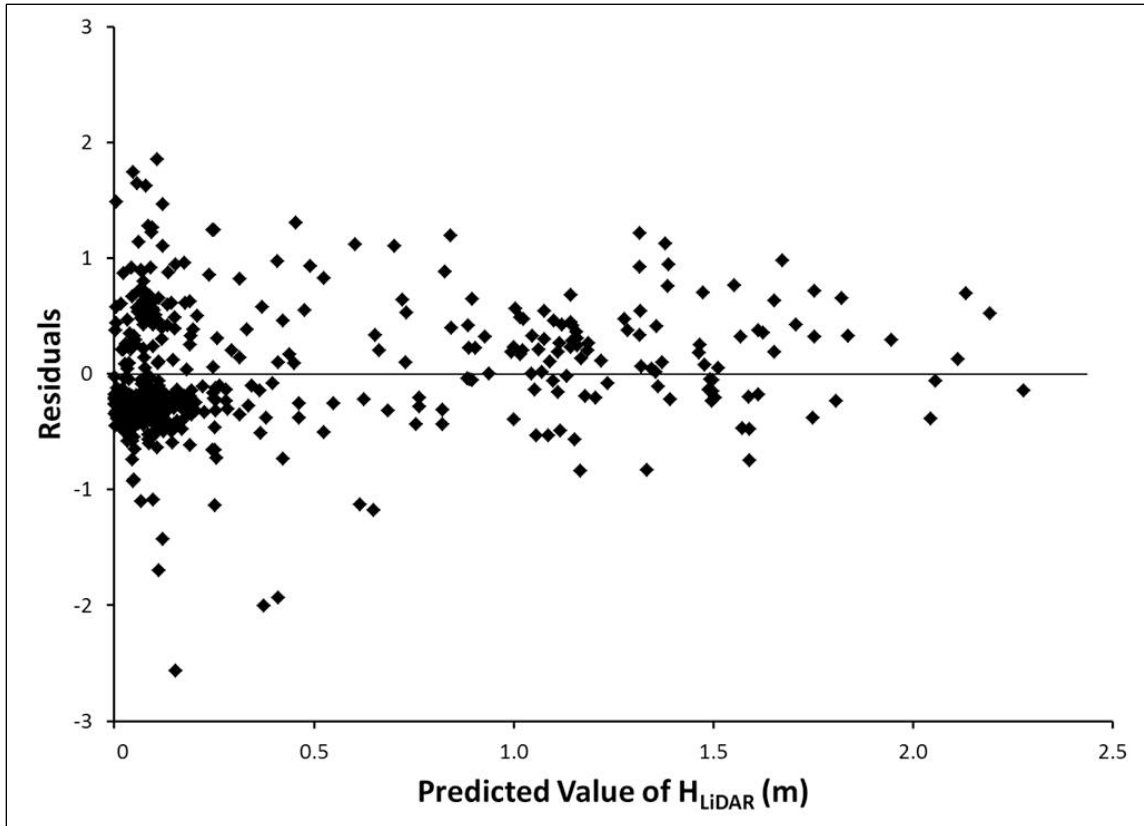
Figure 6. Residuals of the field-measured maximum heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) regression (Fig. 4) plotted with predicted values of H_{LiDAR} for all plants (n = 448). The lack of a random distribution around zero up to H_{LiDAR} of approx. 0.3 m, and the larger spread of the residuals at smaller H_{LiDAR} values indicate that LiDAR may not be effective in predicting heights of smaller-statured plants.
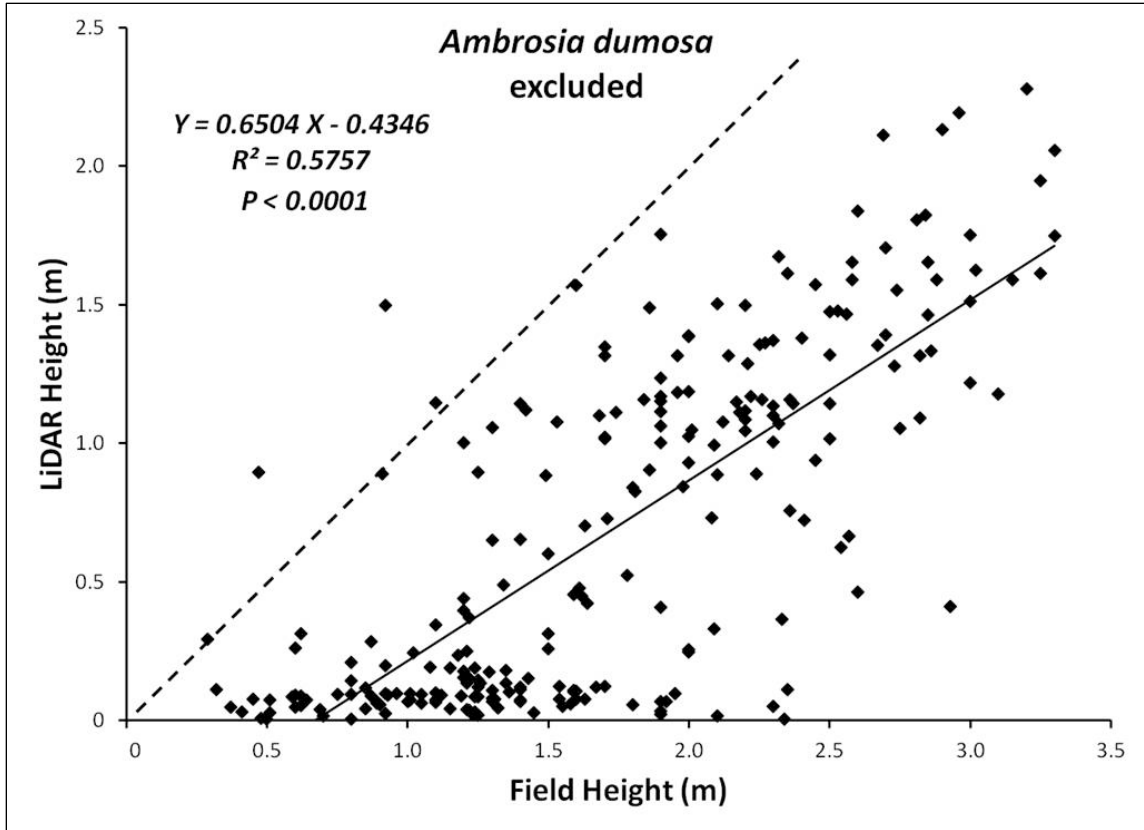
Figure 5. Simple Linear Regression of field-measured maximum heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) for all samples (n = 237) excluding *Ambrosia dumosa*. The solid line represents the best fit linear regression line, while the dashed line represents the 1:1 correspondence. With *Ambrosia dumosa* excluded from the model there is a significant linear relationship ($P < 0.0001$) between H_{Field} and H_{LiDAR} and $R^2 = 0.58$. With the exception of a few samples (points above 1:1 line), LiDAR underestimates actual plant heights.

Spatial Analysis

    Global Clustering. Large plants (1-4 m tall as estimated by LiDAR) were significantly clustered at all spatial scales both above (Fig. 13) and below (Fig. 14) the road, indicated by the observed pattern falling above the 99.9% confidence envelope. Even though clustering was significant both above and below the road, the shape of the *L(d) – d* function distinguished a difference between the two study areas. Above the road, *L(d) – d* increased rapidly only up to ca. 25 m, then very slowly increased across the remaining distances. Below the road *L(d) – d* increased rapidly up to ca. 100 m and

continued to increase up to ca. 270 m where spatial clustering was most pronounced. At

greater distances $L(d) - d$ declined, but always remained at high values of significant

clumping. This contrast in curve-shape indicates that plants below the road were more

closely clustered together, and those above the road tended to be more evenly spaced,

which is apparent when you look at the distribution of LiDAR points across the study

areas shown in Figure 3.
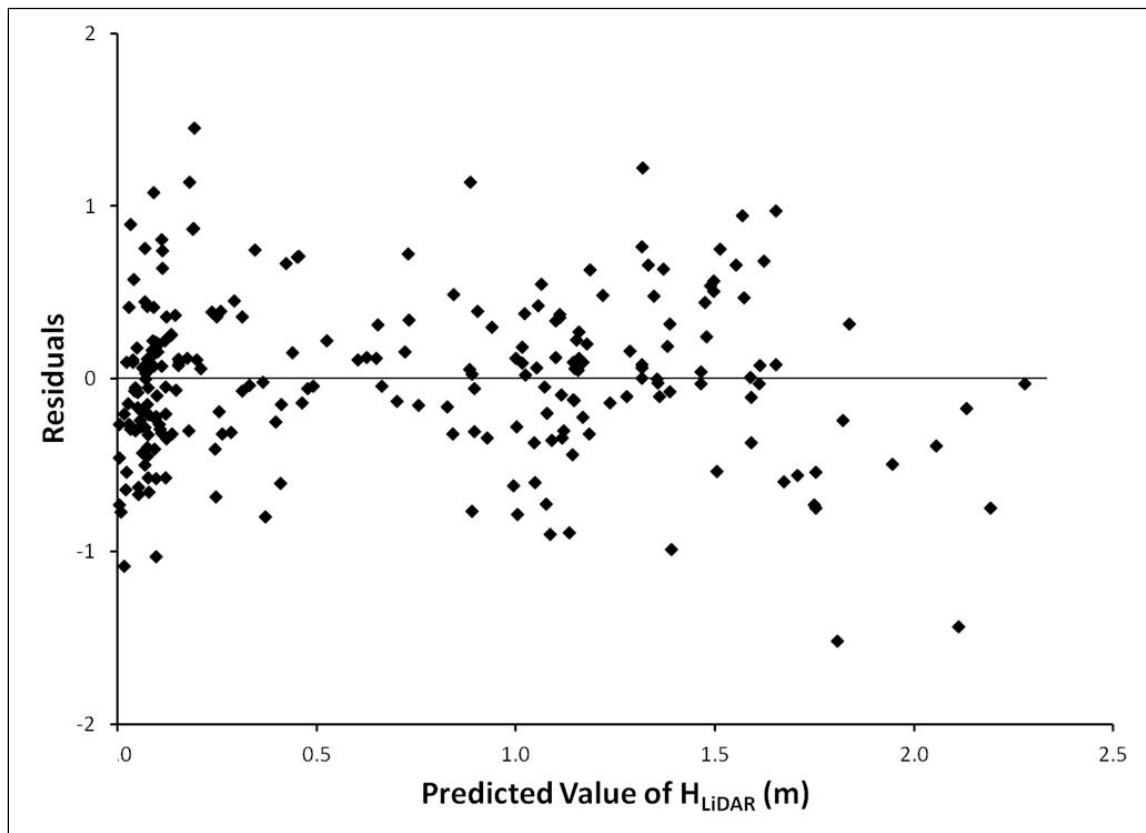
Figure 6. Residuals of the *Ambrosia*-excluded field-measured maximum heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) regression (Fig. 7) plotted with predicted values of H_{LiDAR} for all samples (n = 237) excluding *Ambrosia dumosa*. Heavy clustering of residual values between 0-0.3 m suggests minor biases in the regression owing to small plant sizes.
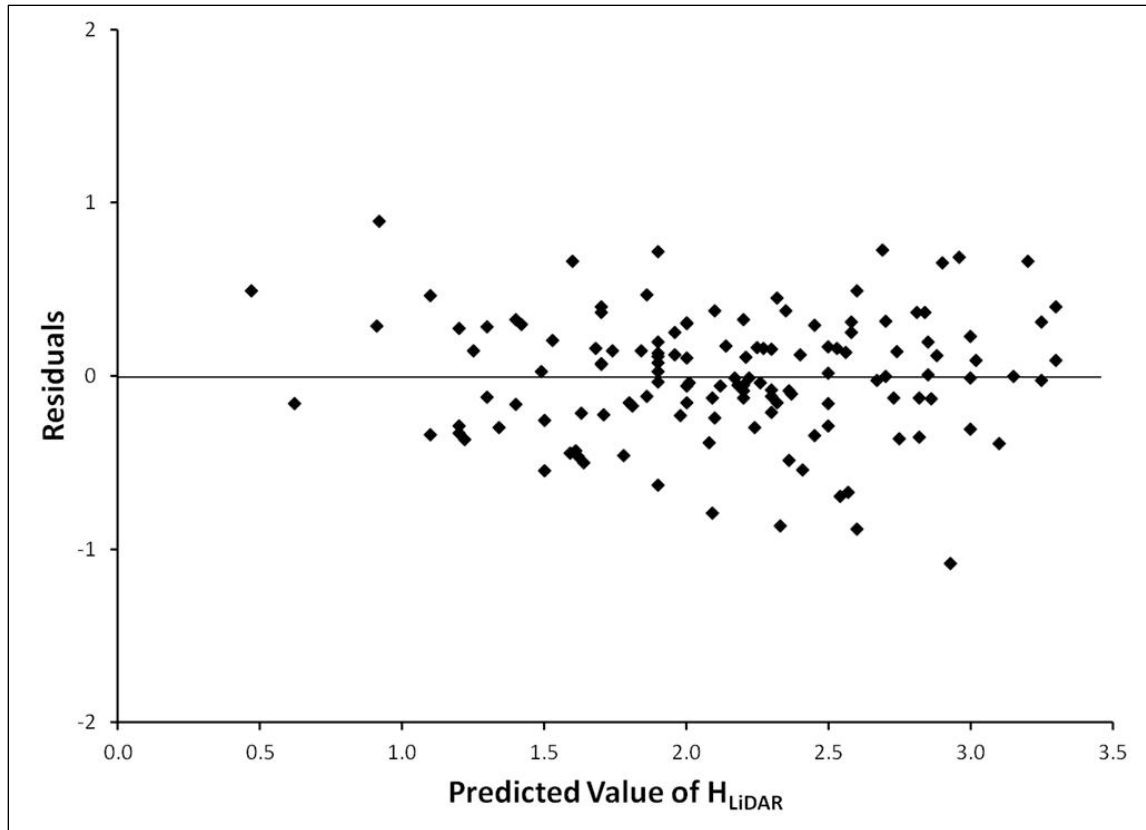
Figure 7. Residuals of the *Ambrosia*-excluded field-measured maximum heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) regression (Fig. 7) plotted with predicted values of H_{LiDAR} but with residuals from measured H_{LiDAR} values of < 0.3 m removed (n = 132). The random pattern around zero suggests that biases in the regression owing to smaller plant sizes have been removed.

This analysis also shows an unexpected result of the confidence envelope not following the expected zero-line (i.e., expected random point process); dropping well below zero in both analyses. Upon further investigation into this problem I found that there have been other cases of this happening when using the Ripley's tool in ArcGIS 10.0. A query of the ArcGIS Online Forum provided responses from ESRI professionals and other spatial ecologists about this occurrence. The confidence envelope should follow the expected outcome when the study area shape is simple, such as a rectangle or circle. However, irregularly shaped study areas, like the ones in this study, can force randomly placed points to be far away from each other, and the confidence envelope will

appear below the expected line. Additionally, a bug has been identified in the Ripley's

tool for ArcGIS 10.0 that when "simulate outer boundary values" for the edge correction

method and "compute confidence envelope" are selected, the edge correction factor is

only applied to the observed values, but not to the confidence envelope lines, resulting in

a drooping confidence envelope. Both of these explanations are plausible for this study;

yet, it has also been suggested that when a point process is not homogeneous, and the null
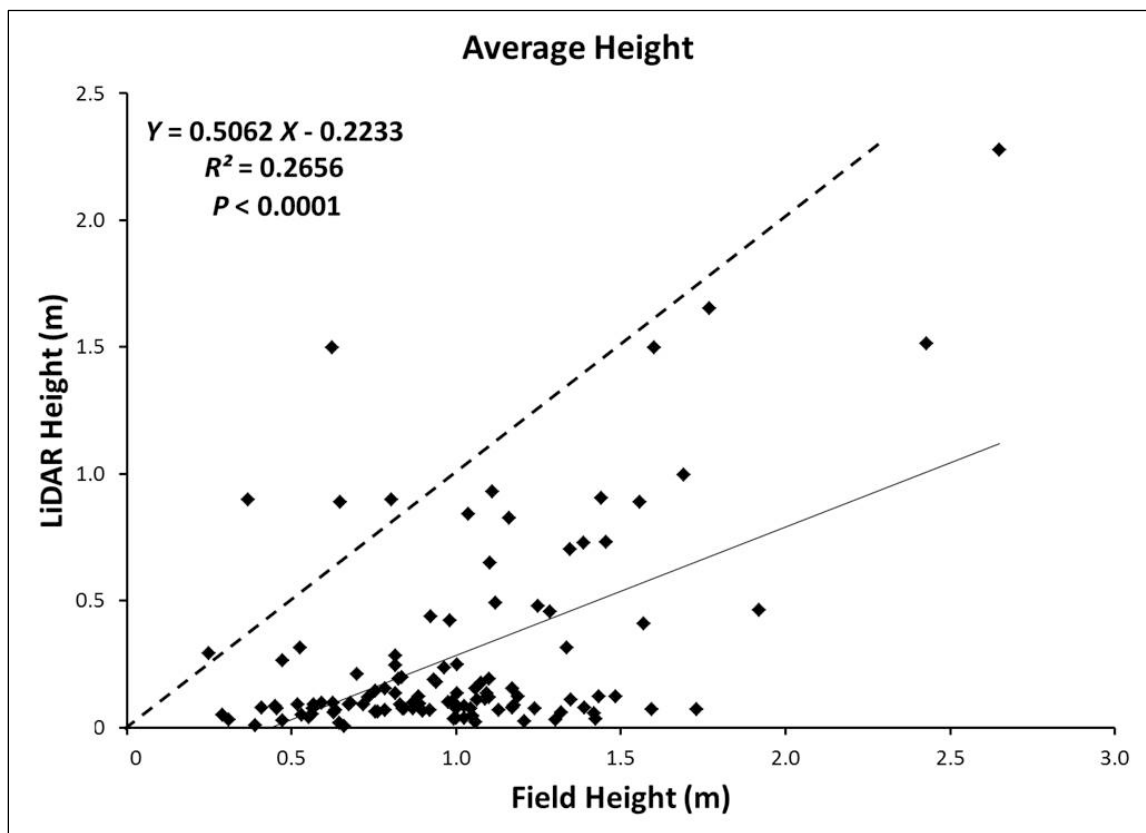
Figure 8. Simple Linear Regression of field-measured average heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) excluding *Ambrosia dumosa* (n = 114). The solid line represents the best fit linear regression line, while the dashed line represents the 1:1 correspondence. There is a significant linear relationship ($P <$ 0.0001) between H_{Field} and H_{LiDAR} and R^2 = 0.27. With the exception of a few samples (points above 1:1 line), LiDAR underestimates actual plant heights.

hypothesis of CSR is invalid, the expected line (not just the confidence envelope) will not follow the randomization process. It has been acknowledged that the plants in my study areas do not represent a homogeneous point process, thus the expected randomized distribution and its confidence envelope may be miscalculated; however, the observed global spatial patterns revealed by the *L(d) – d* curves in this study provide evidence that vegetation patterns are being clearly influenced by different spatial processes above vs. below the road.
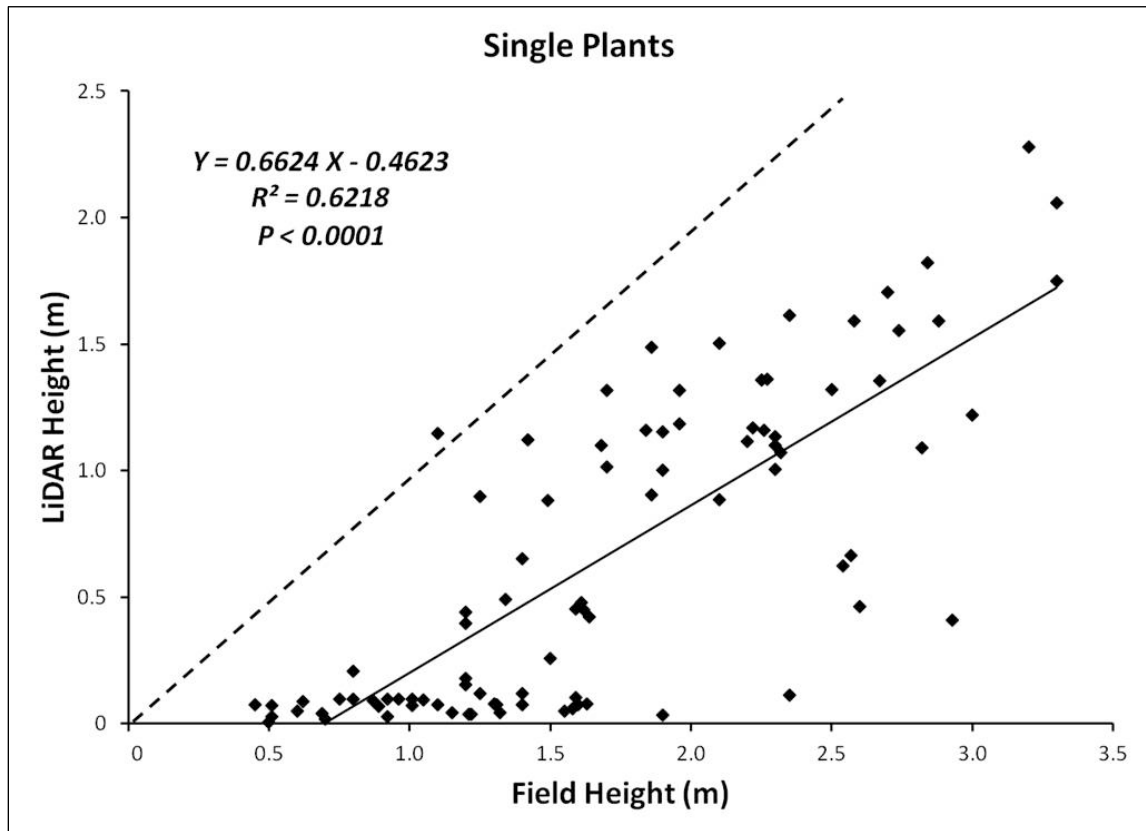
Figure 9. Simple Linear Regression of field-measured maximum heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) for single plants and excluding *Ambrosia dumosa* (n = 89). The solid line represents the best fit linear regression line, while the dashed line represents the 1:1 correspondence. There is a significant linear relationship ($P < 0.0001$) between H_{Field} and H_{LiDAR} and the $R^2 = 0.62$.

Single Plants
Average Height

$Y = 0.6465 \, X - 0.4025$

$R^2 = 0.4752$

$P < 0.0001$
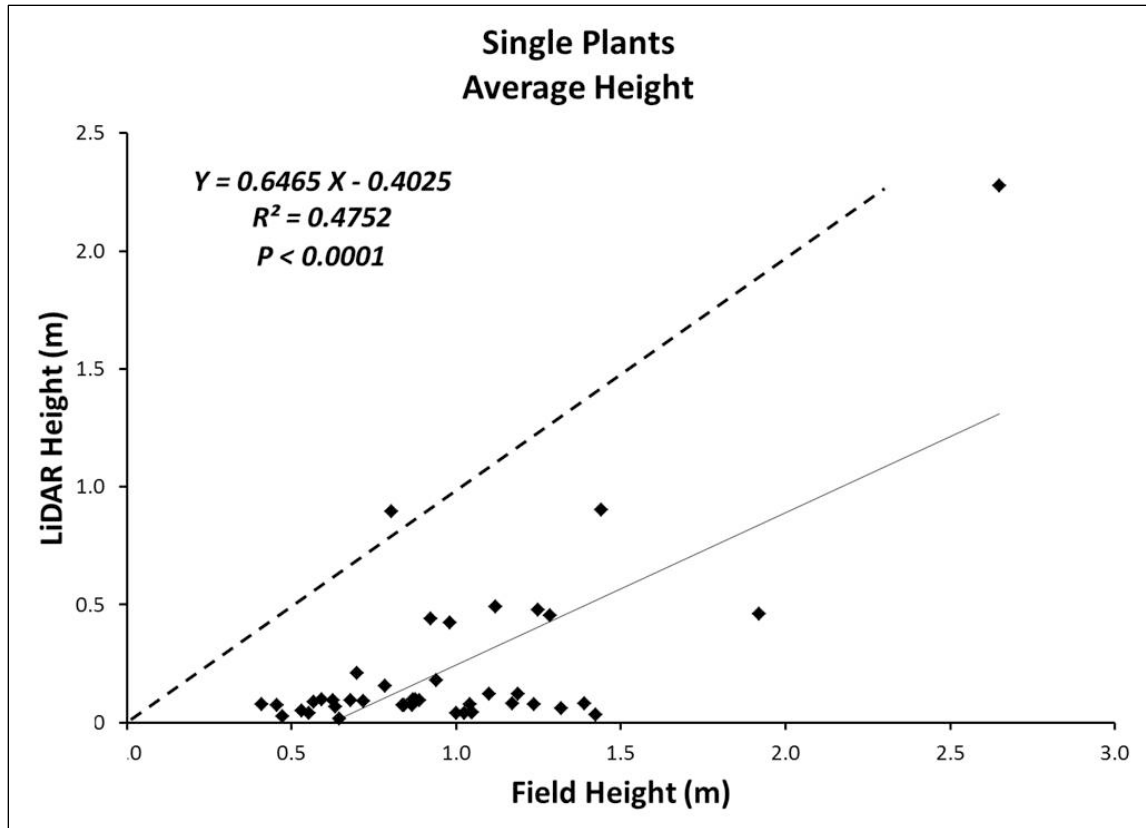
Figure 10. Simple Linear Regression of field-measured average heights (H_{Field}) vs. LiDAR-measured heights (H_{LiDAR}) for single plants and excluding *Ambrosia dumosa* (n = 42). The solid line represents the best fit linear regression line, while the dashed line represents the 1:1 correspondence. There is a significant linear relationship ($P < 0.0001$) between H_{Field} and H_{LiDAR} and the $R^2 = 0.48$.

Local Clustering. Unlike Ripley's *L(d)* analysis, the local Getis-Ord statistic allowed an examination of spatial patterns that does not necessitate the assumption of homogeneity (Getis and Ord 1992). Neighborhoods (20 x 20 m grids) that were members of significant clusters at 10, 50 and 100 m are shown in Figure 15. There were no significant coldspots (neighborhoods with similar low numbers of plants nearby) detected and therefore only hotspots of clustering are shown.
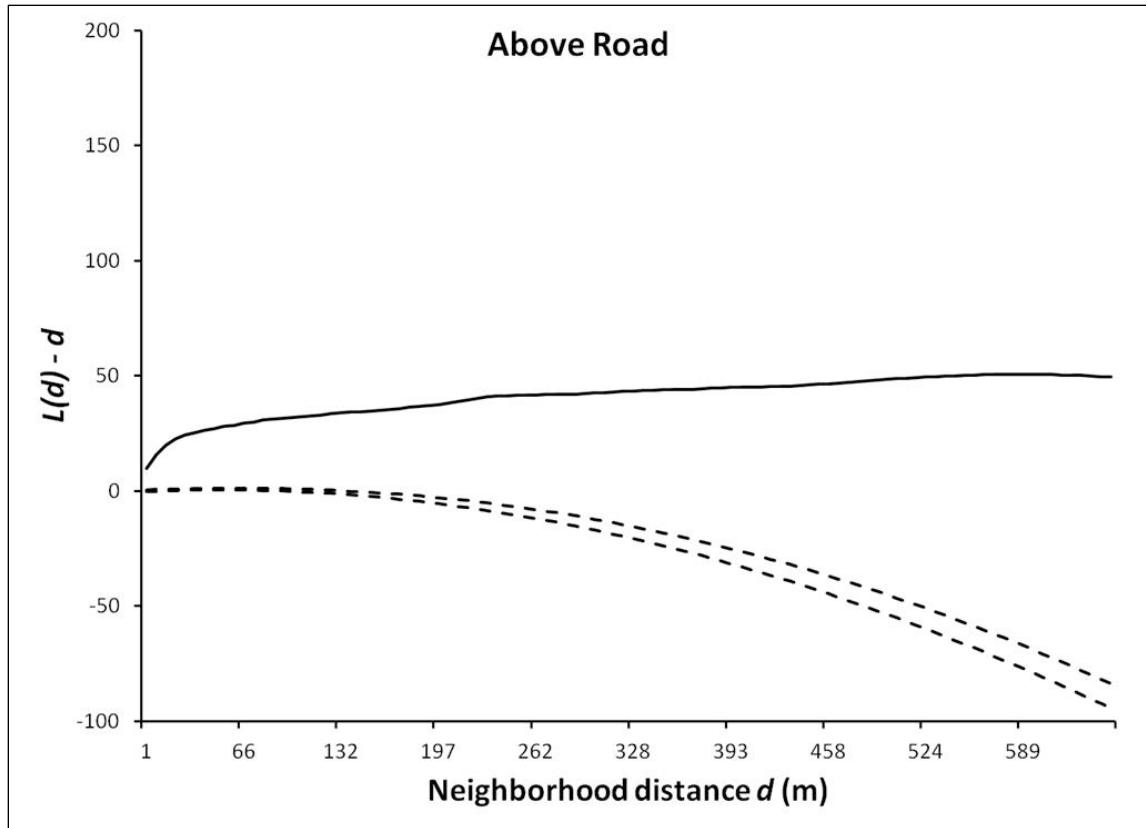
Figure 11. Ripley's *L(d)* analysis of the distribution pattern of large plants (1-4 m tall) above the road. The plot of *L(d) – d* versus *d* (solid line) revealed spatial clustering across all distances, based on departure (above) from the 99.9% confidence intervals (dotted lines) for complete spatial randomness.

Above the road, the majority of neighborhoods that exhibited significant clustering only did so to 10 m, 106 occurrences, with only 54 and 25 neighborhoods exhibiting clustering to 50 and 100 m, respectively. The clusters appeared to be relatively evenly spaced, congruent with the results from Ripley's K-function where *L(d) – d* increases slowly across all spatial distances greater than ca. 25 m (Fig. 13). Below the road, the opposite pattern was observed. There were only 30 occurrences of neighborhoods which exhibited clustering to 10 m, with the number increasing to 40 and 52 neighborhoods with clustering at 50 and 100 m, respectively. In addition, clusters

were more closely aggregated, once again conforming to the Ripley's analysis where *L(d)* – *d* rises rapidly across these distances (Fig. 14).
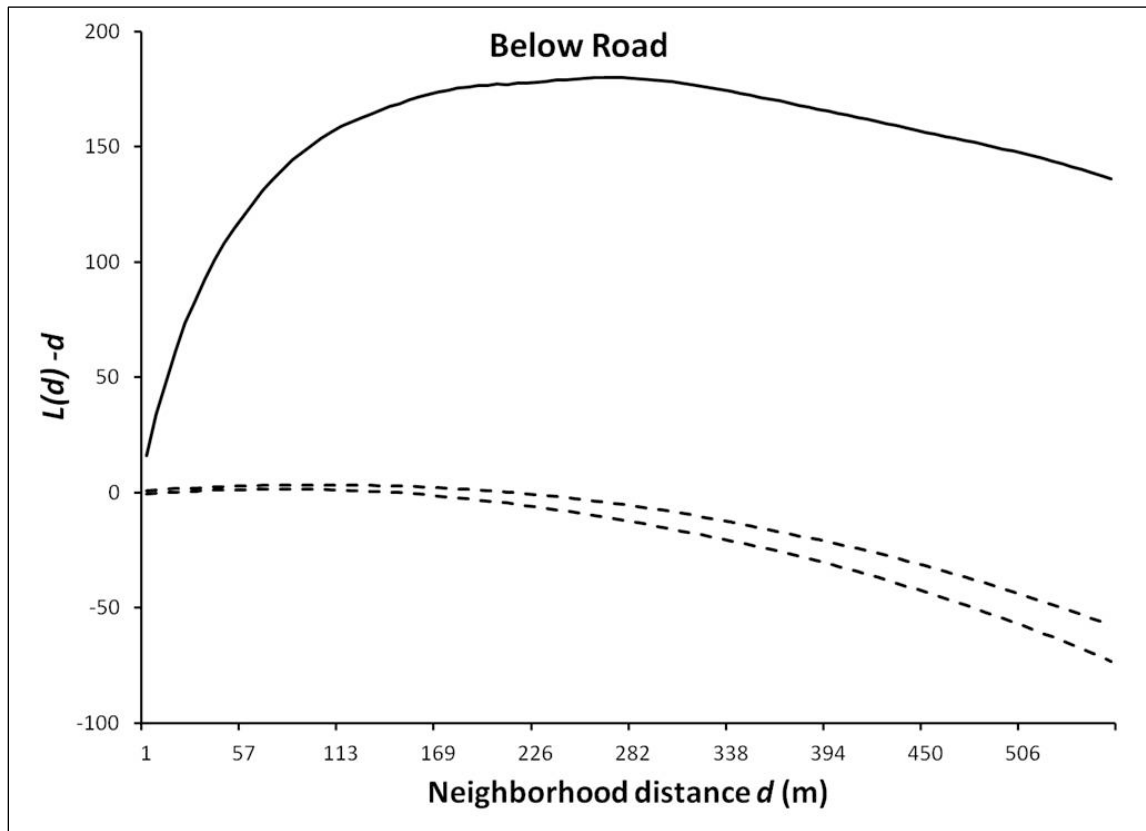
Figure 12. Ripley's *L(d)* analysis of the distribution pattern of large plants (1-4 m tall) below the road. The plot of *L(d)* – *d* versus *d* (solid line) revealed spatial clustering across all distances based on departure (above) from the 99.9% confidence intervals (dotted lines) for complete spatial randomness.

To assess the impact of wash flow disturbance on plant distributions, local clustering was quantified in relation to the study units (Fig. 15). Where wash flow has been uninterrupted (Above Rd) there were only 13 total occurrences of local clustering; seven with clustering only within the neighborhood itself (10 m), four clustered to a neighboring distance of 50 m, and two to 100 m (Fig. 16). The effect of diminished wash flow due to road disturbance was evident by the absence of any plant clusters in Below

Rd – study plots (Figs. 15 and 16). In contrast, where wash flow has been artificially

enhanced by the presence of the road (Below Rd + plots) there was a high frequency of

clustering to a neighboring distance of 100 m (31 occurrences), 14 clustering to 50 m,

and six that exhibited 10-m clustering (Fig. 16). Furthermore, strong plant clustering was

apparent in and adjacent to dominant active washes (Fig. 17), illustrating how the

hydrology and surficial geology of this bajada drives plant spatial distributions.
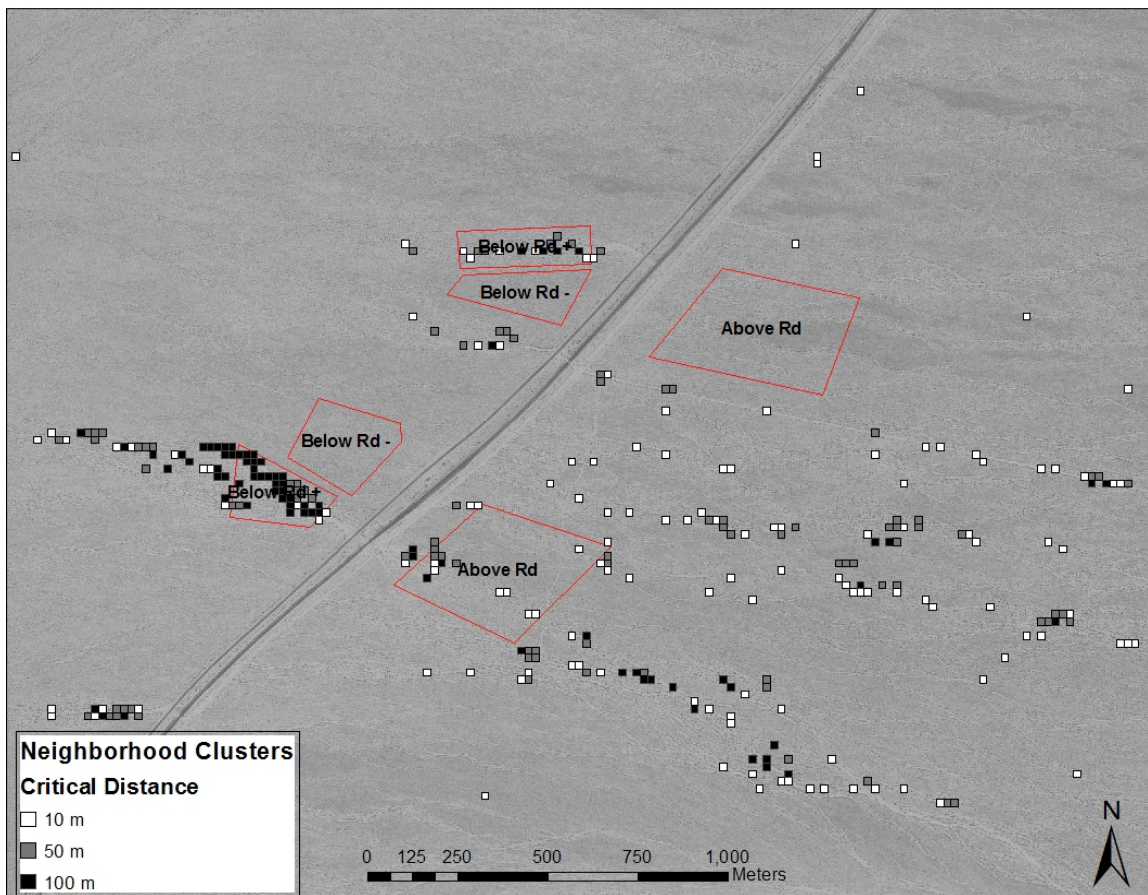
Figure 13. Local clustering (G_i^*) across the Hayden study area. The number of 1-4 m vegetation points in each neighborhood (20 x 20 m grid cell) was used to assess local clustering at critical distances of 10, 50 and 100 m. There are no significant clusters in the Below Rd - study plots, and a high frequency of 100 m clusters in the Below Rd + study plots. Clusters appeared to be more evenly spaced above the road, with fewer significant clusters occurring in the Above Rd study plots.
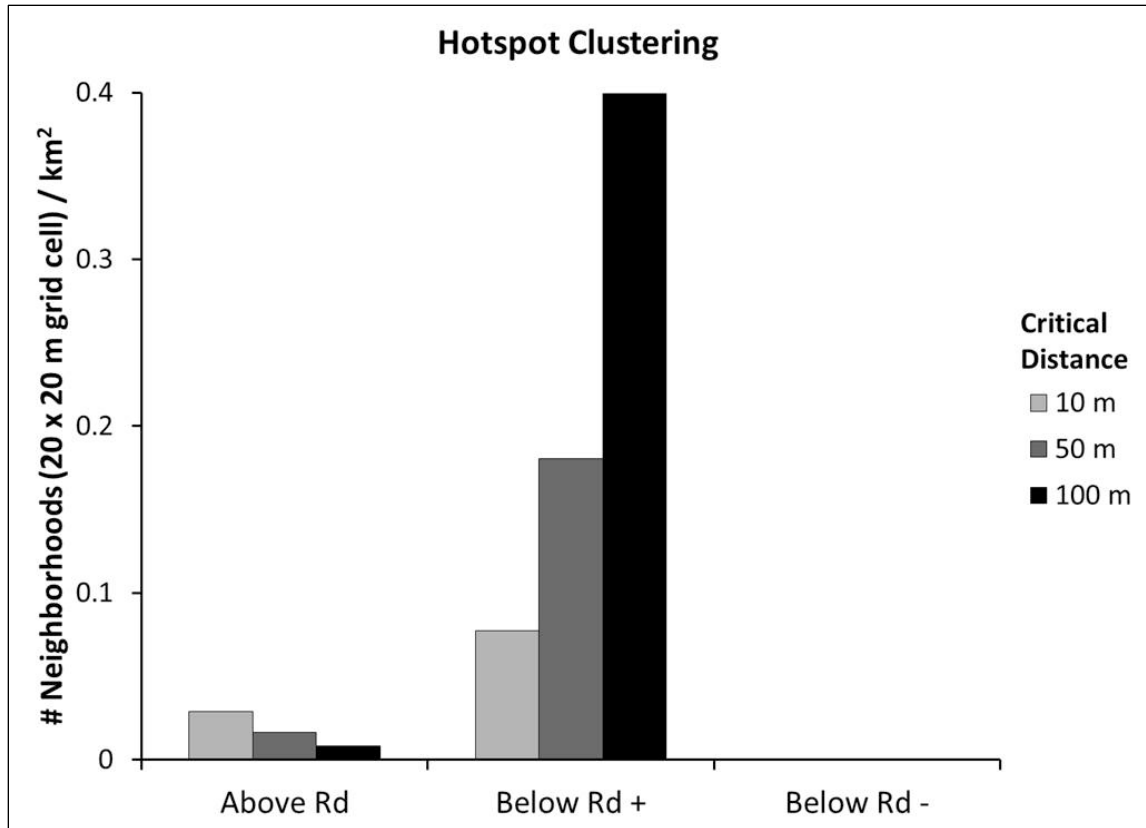
Figure 14. Frequency of hotspot (G_i^*) neighborhoods (number of clusters / km^2) with critical distances of 10, 50 and 100 m found for the three study units; Above Rd (uninterrupted wash flow), Below Rd + (enhanced wash flow due to diversion caused by road), and Below Rd – (deprived wash flow due to diversion caused by road). # neighborhoods represents the number of 20 x 20 m grid cells that have peak clustering at 10 m (significant clustering within neighborhood only) 50 m and 100 m. Significance corresponds to G_i^* values exceeding the 99% confidence interval (*P*-value of 0.01).
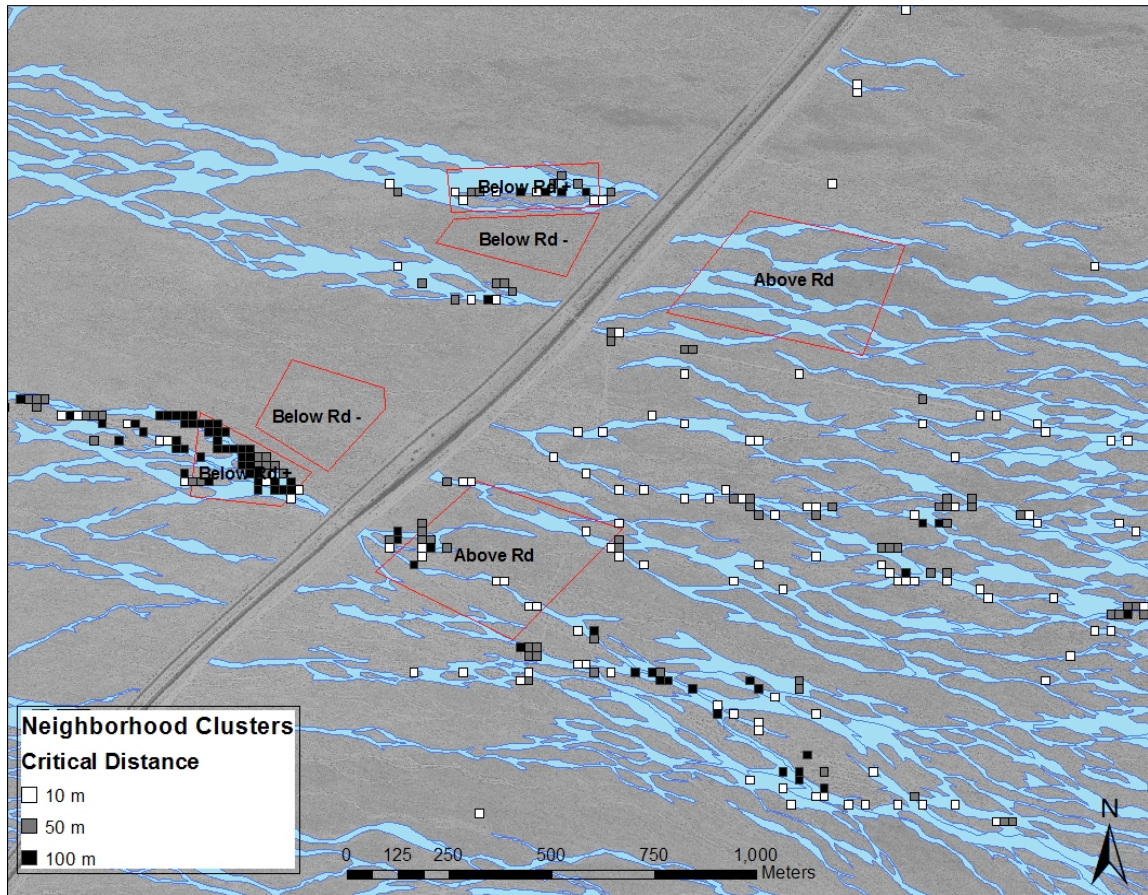
Figure 15. Locations of local clustering (G_i^*) across the Hayden study area with surficial hydrology (washes) shown as blue shading.

Plant Size

There was a significant difference in the mean maximum height of *Larrea* (KW; $P < 0.0001$, $\chi^2 = 25.82$, df = 2) among the three study plot types. Above Rd heights were significantly lower than Below Rd + (Wilcoxon; $Z = -6.84$, $P < 0.0001$) as were Below Rd - vs. Below Rd + (Wilcoxon; $Z = -5.35$, $P < 0.0001$), but Above Rd and Below Rd - were not significantly different (Wilcoxon; $Z = 0.31$, $P = 0.75$). There was not a significant difference in the mean maximum height among the three study units for *Ambrosia* (KW; $P = 0.08$, $\chi^2 = 4.94$, df = 2) (Table 2).

Mean volumes (m³) of single *Larrea* plants were also significantly different among the three study units (KW; $P < 0.0001$, $\chi^2 = 40.62$, df = 2). As seen for height, Below Rd + plants had significantly greater volume than Above Rd (Wilcoxon; $Z = -5.30$, $P < 0.0001$), and Below Rd – plants (Wilcoxon; $Z = -5.02$, $P < 0.0001$); while, Above Rd and Below Rd – plant volumes were not significantly different ($Z = 0.09$, $P = 0.93$). *Ambrosia* showed a similar pattern where the mean volume (m³) of single plants among the three study units were significantly different (KW; $P < 0.0001$, $\chi^2 = 20.83$, df = 2), with Below Rd + plants being significantly larger than Above Rd plants (Wilcoxon; $Z = 4.1$, $P < 0.0001$), and Below Rd - plants (Wilcoxon; $Z = 4.17$, $P < 0.0001$). Similarly to *Larrea*, Above Rd and Below Rd - *Ambrosia* plant volumes were not significantly different ($Z = -0.71$, $P = 0.48$) (Table 2).

Table 2. Maximum height (m) and volume (m³) of *Larrea* and *Ambrosia* plants for the three study units. Sample size (n), mean, and standard error (±SE) are shown. Different letters represent significant differences of the mean within each species across study units at the 0.0167 significance level (multiple pairwise Wilcoxon test with Bonferonni adjustment).

	Maximum Height (m)		Volume (m³)	
	Larrea	*Ambrosia*	*Larrea*	*Ambrosia*
Above Rd	n = 52 $1.33^a \pm 0.07$	n = 61 $0.38^a \pm 0.011$	n = 25 $1.83^a \pm 0.48$	n = 34 $0.08^a \pm 0.009$
Below Rd +	n = 65 $2.22^b \pm 0.07$	n = 36 $0.47^a \pm 0.025$	n = 43 $9.36^b \pm 1.17$	n = 29 $0.30^b \pm 0.087$
Below Rd -	n = 24 $1.36^a \pm 0.09$	n = 114 $0.41^a \pm 0.007$	n = 16 $1.24^a \pm 0.33$	n = 98 $0.09^a \pm 0.006$

Discussion

LiDAR's Ability to Measure Plant Heights

In the analysis quantifying the relationship between field-measured and LiDAR-derived plant heights, it is evident that H_{LiDAR} can be used to predict H_{Field} of *Larrea*

(which constituted the majority of validation points of taller vegetation), but cannot be used to accurately assess heights of *Ambrosia* plants. One possible explanation for the latter is that *Ambrosia* plants may have been dormant due to a dry year when the LiDAR data were collected (October 2004) (Dave Bedford pers. comm.). This would result in laser returns missing the top of canopy, and instead hitting the ground (Rango et al 2000; Streutker and Glenn 2006); however, *Ambrosia* is densely branched which should favor LiDAR returns even when plants are dormant. Another, more plausible explanation, is that there was a minimum plant detection size below which accurate LiDAR returns are more difficult.

With the LiDAR used in this study, it appears that a plant height of 0.3 m was the lower limit of accurate detection in this desert system. Root mean square error (RMSE), a measure of the absolute fit of the model (i.e., how close the observed data points are to the models predicted values), ranged between 0.29 to 0.4 m. Su and Bork (2007) and Mitchell et al. (2011) reported similar RMSE values for the shrub *Elaeagnus commutata* in Alberta, Canada (0.48 m) and for sagebrush (*Artemisia tridentata* subsp. *vaseyana*) shrubs in southeastern Idaho (0.35 m), respectively. This implies that shorter shrubs, such as *Ambrosia* whose average maximum height in this study was ca. 0.40 m, are harder to delineate using LiDAR data compared to larger shrubs such as *Larrea*. This limit is also consistent with the findings of Streutker and Glenn (2006) who found a lack of correlation between H_{Field} and H_{LiDAR} for smaller sagebrush plants. They estimated that 0.20 m was the minimum plant size for LiDAR detection in a low canopy system. These concordant findings suggest that H_{LiDAR} cannot serve as an accurate predictor of plant heights for smaller plants in this desert system.

Difference of Field- vs. LiDAR-Measured Plant Heights. The mean difference between measurement methods ($H_{LiDAR} - H_{Field}$), sometimes called mean error, is often reported in studies assessing the accuracy of LiDAR for determining field measured plant heights. In this study, LiDAR regularly underestimated field heights ($H_{LiDAR} < H_{Field}$). This finding is consistent with similar studies where LiDAR uniformly underestimated plant heights in semi-arid sagebrush rangelands (Mitchell et al. 2011; Sankey and Bond 2011; Streutker and Glenn 2006), as well as mixed shrubland community types in Alberta, Canada (Hopkinson et al. 2005; Su and Bork 2007).

After excluding *Ambrosia*, the mean error in this study was approximately -1.0 m, (i.e., LiDAR underestimates height by 1.0 m) whether using all remaining samples or single plants alone. When average height was used rather than a single maximum plant height, the mean error was reduced by ca. 25% (mean error -0.71 to -0.75 m). This result is probably due to the fact that LiDAR laser pulses often hit branches rather than the absolute top of a plant (Streutker and Glenn 2006). Previous LiDAR studies of shrublands have documented underestimates of ca. 0.3 to 0.4 m in sagebrush communities (Mitchell et al. 2011; Sankey and Bond 2011), 0.04 m for *Elaegnus* (Su and Bork 2007), and 0.39 m to 1.09 m for low shrubs (< 2 m) and tall shrubs (2-5 m), respectively (Hopkinson et al. 2005). Forest studies have reported mean errors in the range of 0.09 m to 1.46 m underestimation (Andersen et al. 2006; Wang and Glenn 2008) and have found LiDAR errors to be greater than errors obtained from conventional field sampling techniques. Nonetheless, LiDAR methods may be valuable in spite of greater error due to the time and cost efficiency of obtaining such information on a large scale. An approximate 0.75 to 1.0 m underestimation as seen in this study is reasonable in forest

settings, but in desert systems where shrubs do not reach heights of much more than 2 m this error limits the ability of LiDAR to accurately assess plant heights of smaller stature, such as *Ambrosia*.

There are many possible explanations for the underestimation of actual plant heights. The approximate 5 year time lapse which occurred between LiDAR data acquisition and the collection of field measurements could account for some of the error due to growth over those five years, but this effect is likely small due to the slow growing nature of *Larrea* (0.75 to 0.98 mm/year) (Vasek 1980). Another source of error could be the misalignment of plants between field and LiDAR due to GPS inaccuracies; however, without a better means to accurately geolocate plants and LiDAR points, the use of a spatial buffer can reduce misalignment errors by corresponding the field-measured maximum plant height with the highest LiDAR point within the specified buffer radius, as LiDAR points rarely represent the absolute top of plant canopies (Streutker and Glenn 2006). Inaccuracies may also exist because LiDAR-derived DSMs rely on data smoothing that occurs when creating DEM products from raw point LiDAR data (Gaveau and Hill 2003). While using raw point cloud data from LiDAR has been suggested to be more accurate than grid-based DEM's in a forested setting (Gaveau and Hill 2003), the predictive strength of H_{LiDAR} was not improved in other low canopy systems ($R^2 = 0.84$ for raw point cloud data; $R^2 = 0.86$ for grid-based data), and the extra time required to work with raw data makes the grid-based approach more desirable (Mitchell et al. 2011).

Insufficient sampling density has also been suggested to increase the underestimation in small-footprint LiDAR data (Gaveau and Hill 2003; Wang and Glenn 2008). However, a lower-than-average point density of 1.2 points / m^2 has been shown to

provide reasonable predictions of plant heights ($R^2 = 0.72$) in a sagebrush system

(Streutker and Glenn 2006), and the predictions were only slightly improved when using

9.46 points / m^2 ($R^2 = 0.86$) (Mitchell et al. 2011). Even at a sampling density of 50

points / m^2, the highest point of a spruce tree was not detected with LiDAR data

(Ronnholm et al. 2004). Thus, although it is possible that a higher sampling density than

that used in this study (4.48 points / m^2) may provide greater predictive ability (higher R^2

value), it is still unlikely that a DSM derived from LiDAR will represent the very top of

this desert canopy. Therefore, some degree of underestimation should be expected.

The more plausible explanation for underestimation of plant heights in this study

is that laser pulses usually penetrate into the canopy to some extent before being returned

(Gaveau and Hill 2003; Streutker & Glenn 2006; Wang & Glenn 2008). This is even

more likely given the diffuse canopy and low foliage density of *Larrea*. Indeed,

Hopkinson et al. (2005) found that the open structure of low shrubs allowed the greatest

penetration (63%) of laser pulses within the canopy when compared to other vegetation

types. Furthermore, foliage orientation could also reduce the chances of laser pulses

hitting the topmost part of the canopy (Hopkinson et al. 2005) as *Larrea* is known to

orient leaves vertically during dry seasons to reduce the amount of intercepted radiation

and increase water use efficiency (Ezcurra et al. 1992).

Choosing the Best Regression Model. When analyzing regression models to

determine which would represent the best fit to the data, the model with the highest R^2

value is desired here as it represents the model in which H$_{\text{LiDAR}}$ best predicts H$_{\text{Field}}$. The

regression with single *Larrea* plants alone yielded the highest R^2 value (0.62), yet this R^2

was only slightly higher than the analysis that included both single and clumps of plants

(0.58). Likewise, RMSE, intercept, slope and mean difference were essentially the same.

Previous studies comparing field and LiDAR height measurements in forest

systems have reported R^2 values in the range of 0.68 to 0.98 (Andersen et al. 2005;

Brandtberg et al. 2003; Gaveau and Hill 2003; Hollaus et al. 2006), but in low canopy

systems R^2 values are more variable. For example, R^2 values have been reported as low

as 0.11 for shrubs < 2 m tall (Hopkinson et al. 2005) and 0.21 for *Elaeagnus* shrubs that

are typically about 3 m tall (Su and Bork 2007). However, higher values are also

common, such as 0.81 for shrubs 2-5 m tall in a boreal wetland environment (Hopkinson

et al. 2005) and 0.72 (Streutker and Glenn 2006), 0.77 (Sankey and Bond 2011) and 0.86

(Mitchell et al. 2011) for sagebrush shrubs. Based on these previous findings, my R^2

values of 0.58 to 0.62 appear reasonable given the relatively low and diffuse stature of

vegetation in the *Larrea-Ambrosia* scrub community.

Results from the models using average height, rather than maximum height,

showed that the R^2 values greatly decreased, from 0.58 to 0.27 for models including plant

clumps, and from 0.62 to 0.48 for single plants. Given that there is a greater probability

of a LiDAR strike hitting a branch closer to the average height than the maximum plant

height, it is not clear why the average height models resulted in lower R^2 values. Lower

sample size (average height was only measured in 2010, resulting in more than 50%

fewer samples), and proportionally more small plants, (LiDAR performs worse predicting

heights of smaller plants, as shown for *Ambrosia*) may be partly responsible for the

difference. Furthermore, sampling in 2010 resulted in many overlapping 2.0 m buffer

areas, in which adjacent plants with a unique average height value used the same

maximum LiDAR point (H_{LiDAR}) for validation. Such errors due to spatial buffers have been noted in other studies and are difficult to eliminate (Streutker and Glenn 2006).

For the purpose of this study the best fit models appear to be those using maximum height of all non-*Ambrosia* samples (n = 237) or of single plants (n = 89), also excluding *Ambrosia*. Both of these models have high R^2 values (0.58 and 0.62 respectively) and meet all assumptions of SLR. The regression equation derived from the former is: H_{LiDAR} = -0.43 + 0.65 H_{Field}, and when rearranged to predict H_{Field} from H_{LiDAR}, H_{est} = (H_{LiDAR} * 1.54) + 0.66 m. Likewise, for single plants the validation regression H_{LiDAR} = -0.46 + 0.66 H_{Field} becomes: H_{est} = (H_{LiDAR} * 1.52) + 0.70 m. The first equation can be applied to plant clumps while the second equation is most appropriately applied to only single plants, both excluding *Ambrosia*. Notably, because the slope and Y-intercept of both equations are very similar, they will yield H_{est} values that are essentially the same across the usual range of *Larrea* heights.

Spatial Patterns of *Larrea tridentata*

The validation exercise indicated that LiDAR is accurate enough to use for analysis of vegetation properties in this desert system, within certain limits; the primary limit being that it should not be used for small-statured (< 0.4 m) plants. As such, I was confident in using LiDAR to evaluate the distribution patterns of vegetation with heights of ca. 1-4 m.

LiDAR-based measurements of 1-4 m plants across the Hayden study site revealed spatial patterns of clustering both above and below the road (Fig. 3). Ripley's global statistic confirmed the clustering of large shrubs (referred to as *Larrea* hereafter since it is the dominant and only large shrub on this landscape) across the bajada.

Clustering of *Larrea* appeared to occur in response to physical properties of the site that likely influence resource availability, a pattern that has been found for other woody species in arid environments (Skarpe 1991).

Plant aggregations are often a direct result of soil substrate, and thus resource, heterogeneity (Phillips and MacMahon 1981; Prentice and Werger 1985; Skarpe 1991). Below the road, resource heterogeneity and plant clustering is pronounced due to the creation of large active washes, where water has been artificially enhanced (Below Rd +), positioned adjacent to areas with many small but inactive washes (Below Rd -). Above the road clustering appears to be occurring as a result of smaller active washes promoting small-scale heterogeneity. Such differences in the microtopography of a landscape have been shown to dictate plant patterns across bajadas in desert regions (Anderson 1971; Barbour et al. 1977). There have been many documented cases of *Larrea* exhibiting clustered dispersion patterns, but these have been variously attributed to vegetative reproduction of smaller individuals, and reduced competition for a limiting resource, namely water (Barbour 1969; Barbour and Diaz 1973; Phillips and MacMahon 1981; Schlesinger and Jones 1984; Woodell et al. 1969). Such biotic factors potentially contribute to the observed clustered patterns seen in this study, but resource heterogeneity appears to be the greater cause (Schwinning et al. 2011).

While clustered patterns of *Larrea* have been well documented, these same studies and others attest to regular patterns as well (Barbour 1969; Fonteyn and Mahall 1981; Phillips and MacMahon 1981; Schlesinger and Jones 1984; Woodell et al. 1969). *Larrea* exhibits traits that have been suggested to facilitate regular patterns such as high seedling mortality, sporadic seed dispersal, long life span, and intraspecific interference

(Fonteyn and Mahall 1981; MacMahon and Schimpf 1981; Phillips and MacMahon 1981; Woodell et al. 1969). Since regular patterns may take many years to develop and are more likely seen in desert shrubs that are long lived and have low seedling recruitment (Fonteyn and Mahall 1981), it is not surprising that *Larrea* has been found to be regularly dispersed in other studies.

Competition for water has also been noted as the primary cause of regular patterns in deserts, and thus low rainfall has been linked with regular dispersion patterns (Anderson 1971; King and Woodell 1973). Woodell et al. (1969) found that *Larrea* tends towards a regular pattern in areas where rainfall is low, and conversely exhibits clustered patterns where rainfall is high. Since the Mojave Desert is the driest North American desert (Barbour 1969) one might expect *Larrea* to exhibit regular dispersion patterns. However, my results showed clustered patterns throughout the Hayden site, both above and below the road. Heterogeneity caused by the presence of washes, coupled with increased soil moisture along these corridors, appears to be the main cause of the clustered patterns at this site.

When clustering was analyzed at a more local scale, and the surficial geology map was overlaid, the effects of wash presence on *Larrea* distributions were further evident. My data show that *Larrea* patterns within the site are strongly dependent not just on the presence of washes, but on water flow through these washes. This is illustrated by the lack of clustering in the Below Rd – study plots, where even though washes are present, wash water has been significantly reduced over the past 100+ years. In contrast, many clusters were found to be concentrated alongside active washes both above and below the road, although there are places above the road (e.g., northern Above Rd plot) where no

significant clusters exist despite the presence of active washes (Fig. 17). It is not clear why clusters are devoid in these Above Rd areas of the bajada, but because surficial geology has also been deemed a primary determinant of *Larrea* distribution in this system (Bedford et al. 2009), the interaction of wash activity and surface hydrology may be responsible for such variability above the road. Nonetheless, my results and those of others indicate that plant patterns in this system provide a reasonable temporal record of soil moisture (Miller et al. 2009), and as such plant clusters may be useful as a proxy for surface hydrology and predicting wash activity.

Additionally, local analyses of plant patterns may provide a way to quantify the footprint of wash influence on surrounding vegetation. For example, above the road *Larrea* plants cluster at most to distances of 10 m and to a lesser extent out to 100 m, with the opposite pattern below the road, which is possibly a function of water input and wash size. Since relatively more water flows through large washes, such as in Below Rd + areas, there is more water-per-linear distance (i.e., wash edge) and thus larger plants along these wash margins, as shown in this study and others (Schwinning et al. 2011). As such, canopy overlap will be more extensive, thus increasing neighborhood size (i.e., to 50 and 100 m) and larger washes will have a proportionally greater influence on the spatial extent of plant clustering along wash edges.

Sampling Errors

Larrea presents some challenges when defining individuals due to its clonal growth pattern (King and Woodell 1984), and the determination of an individual vs. a clump of plants, that may lead to errors in the analyses of plant distribution patterns (Ebert and McMaster 1981; King and Woodell 1984). Barbour et al. (1977) found that

Larrea shrubs commonly occur in clumps with overlapping canopies, clouding the distinction of individual plants. In this study, roughly 57% of *Larrea* grew in close association with other *Larrea* and *Ambrosia* forming plant clumps, a distinction that can only be made with on-the-ground sampling. Schlesinger and Jones (1984) compared two methods for measuring *Larrea*, the soil-mound approach that identified an individual when all stems emerged from a distinct soil mound, and the stem-cluster approach in which clusters of stems > 25 cm apart were classified as individuals. For the former method, *Larrea* exhibited regular or random patterns, and for the latter, clustered patterns were observed. Ebert and McMaster (1981) believe that regular patterns are rare in nature and that sampling by the soil-mound approach results in the misperception of regular patterns of *Larrea*. Alternatively, one could argue that the stem-cluster approach could lead to erroneous conclusions of clustering. The uncertainties in identifying individual *Larrea* plants, and thus inconsistent sampling procedures, have led to ambiguity in the distinction of *Larrea* patterns. This demonstrates the need for a rigorous method to delineate individuals of *Larrea* before spatial analyses can be used to aid in understanding the underlying causes of *Larrea* patterns.

In the current study each 1-4 m LiDAR point that occurred in a 1 x 1 m grid was counted as an individual; however, a cluster of points (adjacent points) could actually be a single plant. As such, this method could result in the misperception of a clustered pattern when, in fact, only one plant was present across samples. The use of high resolution satellite imagery combined with LiDAR-determined canopy height models may improve the ability to distinguish individual canopies of *Larrea* (Koukoulas and Blackburn 2005), but detecting clumps of plants may still be challenging due to

overlapping canopies. Since there is a certain amount of error associated with using LiDAR data to identify individual vs. clumps of plants, a ground based survey approach should be used in conjunction with LiDAR to validate the conclusion of regular or clustered patterns in desert systems.

An alternative approach is to consider each sample (grid cell) simply as vegetation rather than individuals. This method then only evaluates clustering as a canopy pattern, and can make no inference about plant interactions. Despite these caveats, there is a clear pattern of disturbance that has altered the natural hydrological regime across this desert bajada. These changes, in turn, have significantly altered vegetation distribution patterns that underscore the effect of wash disturbance on the dominant shrub community in the Mojave Desert. It is evident from this study that the hydrology and geology of the landscape drive the spatial distributions of plants, and that desert shrub patterns are highly dependent on the distribution of washes and the flow of water through them.

<u>Plant Size</u>

Larrea shrubs were significantly larger in terms of both height and volume in Below Rd + study areas when compared to both Above Rd and Below Rd - areas. This is not surprising since the depletion of runoff (i.e., Below Rd -) has been reported to significantly reduce *Larrea* cover (Schlesinger and Jones 1984), whereas increased soil moisture has been found to significantly increase *Larrea* height and width (Balding and Cunningham 1974; Johnson et al. 1974). Increased soil moisture derived from runoff is known to have a positive effect on the growth and survivorship of *Larrea* (Schlesinger and Jones 1984; Schwinning et al. 2011), thus as runoff is redistributed under the railroad

and concentrated into large washes below the road, this increased water availability ultimately leads to faster growth rates. *Larrea* has also been shown to favor weakly developed, non-compacted soils that facilitate rapid infiltration of water into deep soil layers (Bedford et al. 2009; Hamerlynck et al. 2002; Prose et al. 1987), much like those in the Below Rd + areas. Plant volume in the Below Rd + areas measured 5 and 7.5 times greater than Above Rd and Below Rd – areas, respectively, consistent with greater water input and variation reported across geomorphic surfaces that have different infiltration rates (Hamerlynck et al. 2002). *Ambrosia* exhibited a similar trend as *Larrea* with significantly larger individuals in Below Rd + areas when compared to Below Rd - or Above Rd areas (although plant height was not significantly different).

Physical Disturbances in the Mojave Desert

Disturbances caused by roads and substrate alterations in deserts have been found to have a significant effect on plant productivity and ultimately could impact community composition in such ecosystems (Bolling and Walker 2000; Johnson et al. 1975; Prose et al. 1987; Schlesinger and Jones 1984). In greater detail, I have shown that the presence of a road and railroad over the past 100+ years has significantly altered vegetation patterns due to changes of wash flow across a portion of the Hayden piedmont in the Mojave Desert. This study demonstrated both positive and negative impacts on the community structure and plant growth of dominant Mojave Desert shrubs, but the study does not indicate large-scale successional changes in vegetation. Although this result may seem surprising due to the highly manipulative nature of the disturbance, successional patterns of long-lived perennial species usually occur over time scales of at least 500-1000 years (Bolling and Walker 2000) or are associated with dramatic or

prolonged climatic changes (Pavlik 2008). Thus, what seems to be a long-term disturbance with evident consequences may actually be relatively young for this type of ecosystem.

Human population growth and urban expansion are current threats to Mojave Desert ecosystems. More recently, there is an increasing demand for alternative energy projects that would necessitate the construction of new roads, which as seen here have a significant effect on the hydrology of desert landscapes and thus plant performance. Furthermore, roads act as vectors for the transport of non-native species. As such, resource-rich microenvironments, such as those in Below Rd + seen in this study, may be more susceptible to such invasions and possibly an increase in fire frequency, which could ultimately impact overall community composition. Such human influences compounded with expected changing climatic conditions have the potential to make a disturbance, such as the one seen in this study, have even greater consequences over the next 100 years and beyond.

CHAPTER 3

INFLUENCE OF SIMULATED SUMMER WASH FLOW ON THE
PHYSIOLOGICAL FUNCTIONING OF DOMINANT MOJAVE DESERT SHRUBS

Introduction

Water inputs are the primary driver of ecological processes in desert ecosystems

(Noy-Meir 1973). Across desert bajadas, small washes (ephemeral stream channels) are

a minor component of the landscape, but are important geomorphic features because they

potentially have the greatest influence on soil water input. Indeed, such washes have

long been recognized as microhabitats with enhanced plant productivity (Balding and

Cunningham 1974; Ehleringer and Cooper 1988; Hillel and Tadmor 1962; Odening et al.

1974), as water availability to plants along wash margins is enhanced due to runoff from

adjacent inter-wash surfaces (Miller et al. 2009; Nimmo et al. 2009; Walter 1963).

Additional favorable characteristics of washes include high infiltration rates (Miller et al.

2009; Nimmo et al. 2009), enhanced water storage (Atchley et al. 1999; Ehleringer and

Cooper 1988; Schmitt et al. 1993), catchment areas for runoff (Hillel and Tadmor 1962;

Griffiths et al. 2006; Schwinning et al. 2011), and a competition-free zone for roots of

plants along wash margins (Schwinning et al. 2011).

The persistence of soil water and its distribution in the soil profile are of great

significance in desert systems as they strongly influence plant available water and thus

plant performance (Ludwig and Whitford 1981; Nimmo et al. 2009). Runoff into washes

and lateral redistribution of water facilitates increased water availability in lower soil layers (Tietjen et al. 2009). Although there is a large amount of water lost through evaporation at the wash surface (Schmitt et al. 1993; Smith et al. 1995), washes also exhibit many properties that enhance soil moisture availability and in turn plant water availability. Young active washes usually have a soil structure with high permeability which enables water to enter the sub-surface and extend several meters down into the soil profile where it remains available for use by deeply rooted perennial plants (Hillel and Tadmor 1962). This increased availability has been reported to positively affect desert plant physiological functions such as higher water status and gas exchange rates (Atchley et al. 1999; Smith et al. 1995). These patterns underscore the importance of washes in the hydroecology of desert landscapes.

Precipitation and Runoff in the Mojave Desert

Precipitation in North American deserts is highly variable, both spatially and temporally (MacMahon and Schimpf 1981). The Mojave Desert is the driest desert in North America with winter rainfall accounting for 82% of the total annual precipitation (Hereford et al. 2006). Winter rainfall events occur over a broad geographic range, are low in intensity, and long in duration. In contrast, summer rains are more localized and shorter in duration, but occur with a much higher intensity (Miller et al. 2009; Thames and Evans 1981).

Historically, summer rains in the Mojave Desert have been thought to have little significance in terms of productivity (Beatley 1974) and have even been suggested as ineffective to shrubs (Odening et al. 1974), while winter rains have proven to be more 'biologically useful' in deserts where winter rainfall dominates (Ogle and Reynolds 2004;

Reynolds et al. 2004). This perception is most likely attributed to the different nature of these storms and how they affect soil moisture.

Summer convective storms produce rapid runoff into washes because the high rainfall rate often exceeds the infiltration rate of interfluvial (between-wash) substrates. This is largely because interfluvial surfaces are comparatively old, and have become more consolidated over time. As such, summer rainfall events usually wet only the top few cm of these more developed soil surfaces, and this moisture can then be easily lost due to high temperatures causing high evaporation (Franco et al. 1994). By contrast, water flowing or running into washes can infiltrate more rapidly (because the substrate is typically young and unconsolidated) and extend deeper into the soil profile where it may be available for uptake by perennials growing along wash margins.

In the Mojave Desert, large washes flow only every 2.6 to 7.3 years, averaged over the past 100 years (Griffiths et al. 2006) with greater frequency occurring as wash size decreases. The frequency and timing of these potentially important wash flow events are highly variable, but usually occur during high-intensity summer storms that fall either upslope or locally where runoff is generated from adjacent stabilized surfaces (Atchley et al. 1999; Ehleringer and Cooper 1988).

Precipitation Changes in the Mojave Desert

Despite evidence that the Southwest United States is experiencing a regional, prolonged drought (Hereford et al. 2006; Karl et al. 2009), some climate models for the 21st century predict that the largest increases in extreme weather events will occur in the arid Southwest, altering both winter and summer precipitation patterns (NAST 2000). Average annual precipitation in the U.S. has increased 5-10% in the past 100 years,

which has been attributed to increased frequency and intensity of rainfall events

(Easterling et al. 2000; Karl & Knight 1998; NAST 2000). Climate models are predicting

increased frequency and intensity of rainfall events in Southwest deserts (NAST 2000),

and hence an increase in wash flow events. Climate changes that increase the frequency

and magnitude of summer rainfall events in the Mojave Desert would increase infiltration

opportunities and water availability for plant use (Campbell and Harris 1981). Such

changes could ultimately alter vegetation composition (Tietjen et al. 2009) and structure

(MacMahon and Schimpf 1981), especially in arid ecosystems where a small change in

the quantity or seasonal distribution of rainfall would represent a large proportional shift.

Experimental Goals

To investigate how plants in the Mojave Desert respond to a large pulse of

summer precipitation, we simulated wash flow that would occur following an early

summer rain event by distributing ca. 2000 gallons of water through a fire hose down a

30 m stretch of a 1-m wide wash. Specifically, this replicated wash flow that would

occur down-slope on an alluvial fan when an isolated summer rain storm occurs higher-

up and, in which no surfaces adjacent to the wash received water. Several previous

studies have quantified summer precipitation use by desert shrubs in response to

simulated localized events (Barker et al. 2005; BassiriRad et al. 1999; Lin et al. 1996;

Ogle and Reynolds 2002; Schwinning et al. 2002; Schwinning et al. 2003; Snyder et al.

2004), or by measuring plant responses to natural summer rain events (Ehleringer et al.

1991; Franco et al. 1994; Hamerlynck et al. 2000); but none of these studies specifically

examined the effect of runoff into washes. As such, limited information exists on how

plants utilize water derived from water pulses in washes.

I investigated how morphologically distinct desert shrubs differed in their physiological response to a pulse of wash water through direct measures of plant water relations. The two shrubs used in this study were *Larrea tridentata* (D.C.) Cov. (Zygophyllaceae) (creosotebush), a large evergreen shrub, and *Ambrosia dumosa* (Gray) Payne (Asteraceae) (white bursage), a small drought-deciduous shrub (hereafter referred to as *Larrea* and *Ambrosia*, respectively). The objectives of the present study were to (1) quantify the responses of these two species to a simulated wash flow event that is similar to what would occur during a summer precipitation event; and (2) assess how these responses vary between species and based on plant proximity to the wash. These measures will allow us to quantify the influence of washes on plant water availability in desert bajada landscapes and, specifically, how runoff events in these washes affect plant activity.

Hypotheses and Predictions

I hypothesized that plant ecophysiological responses to a simulated pulse of wash water will covary with distance from wash, but vary in relationship to morphological and phenological differences between *Larrea* and *Ambrosia*. I predict that plant water potential and leaf stomatal conductance values will be highest in plants closest to the wash after the simulated pulse event; however, *Larrea* is expected to respond at distances farther than those of *Ambrosia* due to their more extensive lateral root system (Brisson and Reynolds 1994; Cannon 1913; Chew and Chew 1965; Gile et al. 1998; Singh 1978). *Larrea*, a larger shrub, has been shown to have lateral roots extending anywhere from 2 to > 4 m (Brisson and Reynolds 1994; Cannon 1913; Chew and Chew 1965; Gile et al. 1998; Singh 1978) while roots of smaller *Ambrosia* have been found to extend greater

than 1 m (Cannon 1911; Wallace and Romney 1972), with the maximum reported length of 1.6 m (Cannon 1913).

Larrea is also expected to respond more rapidly than *Ambrosia* because it exhibits a stress-tolerance strategy allowing it to remain physiologically active all year (Miller et al. 2009; Naumberg et al. 2003; Odening et al. 1974; Schwinning and Ehleringer 2001; Smith et al. 1997) and maintain carbon uptake under very low water potentials (Odening et al. 1974; Lambers et al. 2006). In the Mojave Desert, *Larrea* remains active at water potentials that are, on average, -5.6 to -7.3 MPa (Bamberg et al. 1975; Oechel et al. 1972), but can persist when values are as low as -8.0 MPa (Odening et al. 1974). *Ambrosia* is a drought-avoider, a growth strategy for which the plant drops its leaves and remains dormant when there is not sufficient water for new growth. *Ambrosia* has been shown to enter dormancy when water potentials reach -5.0 MPa (Bamberg et al. 1974), however, when sufficient water is made available *Ambrosia* quickly takes it up (Odening et al. 1974; Lambers et al. 2006), produces new leaves, and increases water potential. *Larrea* and *Ambrosia* have both been found to respond to summer rain events in the Mojave Desert with increasing water potentials (Fonteyn and Mahall 1981), therefore I also predict that both *Larrea* and *Ambrosia* will have the ability to take up water from the summer pulse events and will undergo a rapid increase in water potential (pre-dawn and mid-day) following the pulse event.

In conjunction with the uptake of pulse water and increased water status, I expect *Larrea* and *Ambrosia* to undergo a rapid increase in stomatal conductance, but I predict *Ambrosia* will eventually have greater stomatal conductance than *Larrea*. This is because drought-deciduous plants typically have higher transpiration rates and greater

stomatal conductance during favorable conditions (Bamberg et al. 1975; Smith et al. 1997), and a lower water use efficiency (WUE) (Lambers et al. 2006). Under similar conditions, evergreen shrubs typically have lower transpiration and higher water-use efficiency (WUE) than deciduous shrubs (Ehleringer and Cooper 1988).

<div align="center">Methods</div>

Study Site

  The study took place on the Hayden piedmont within the Mojave National Preserve at a site (35°02'N, 115°36'W, elevation 792 m) approximately 50 km SE of Baker, CA and 5 km NE of the Kelso, CA train depot. The Hayden piedmont is at the foot of the Providence Mountains and the study site is upslope from Kelso-Cima Rd and the adjacent railroad (Fig. 1). The plant community at the study site consists of *Larrea tridentata-Ambrosia dumosa* desert scrub, a community type that occupies approximately 70% of the Mojave Desert (Thames and Evans 1981). *Larrea* and *Ambrosia* were selected as the study species because of their wide distribution and co-dominance in the Mojave Desert, and for their differences in life form, leaf phenology and rooting patterns (Lambers et al. 2006; Reynolds et al. 2004; Smith et al. 1997).

  The geology of the Hayden piedmont is classified according to age and depositional process, and in my study area, Quaternary young alluvial fan deposits, Qya (Holocene and late Pleistocene), and intermediate alluvial fan deposits, Qia (late to middle Pleistocene) are present (Bedford 2003; Miller 2012). The geologic substrate of the specific study site was, Qya4, a young deposit 9-15 kyr old with typically weak, sandy Av, Bw, and calcic stage I horizons, bisected by a small ephemeral wash (Qya1: 0-20 year old deposits of loosely sorted sand and gravel) (Bedford 2003; Miller et al. 2009).

Analysis of the wash soil profile (0-100 cm) revealed three layers of different age and origin (David Miller, USGS Menlo Park, CA, pers. comm.). The top ca. 17 cm is the active wash (A) sediment consisting of loose gravelly sand with no roots present. The active wash sediment overlies early Holocene alluvial fan sediment (Bw) to a depth of ca. 35 cm that is laterally continuous with adjacent Qya4 deposits. Older Pleistocene alluvial fan sediment (2Bw) is present at ca. 50-65 cm depth. Stage I calcic horizons were present at ca. 35-50 cm and ca. 65-90 cm depth with stage II calcic cementing at > 90 cm depth. Roots were found in the greatest densities at 28 and 51 cm depth (Appendix 1).

Temperature, precipitation and relative humidity data were obtained from weather stations located at the Hayden piedmont operated by the USGS, Menlo Park, CA (Fig. 18). Mean daily temperatures during the year of study (1/1/2009-12/31/2009) ranged from 1.5°C in winter to 36.9°C in summer. Maximum air temperature during the 2009 sampling period (6/1/2009-9/29/2009) ranged from ca. 25°C to ca. 45°C (Fig. 18A), and mean relative humidity ranged from ca. 3% to ca. 48% (Fig. 18B). Climate records from 2002-2008 indicate highly variable inter- and intra-annual precipitation with average annual precipitation of 127 mm yr^{-1} (range 56 to 205 mm yr^{-1}). Cool season precipitation (Oct-April) averaged 92 mm yr^{-1} (range 43 to 177 mm yr^{-1}), and warm season (July-Sept) averaged 44 mm yr^{-1} (range 10 to 97 mm yr^{-1}). In 2009, the total annual precipitation was 69.2 mm, with summer rain (July-Sept) representing 37% of the total precipitation (25.8 mm) (Fig. 18A). Natural summer precipitation events occurred on July 2 (5.4 mm), July 23 (1.4 mm), July 24 (6.4 mm), July 25 (0.2 mm), August 23 (11.8 mm), and Sept 4 (0.6 mm) (Fig. 18A); none of which generated wash flow at my study site.
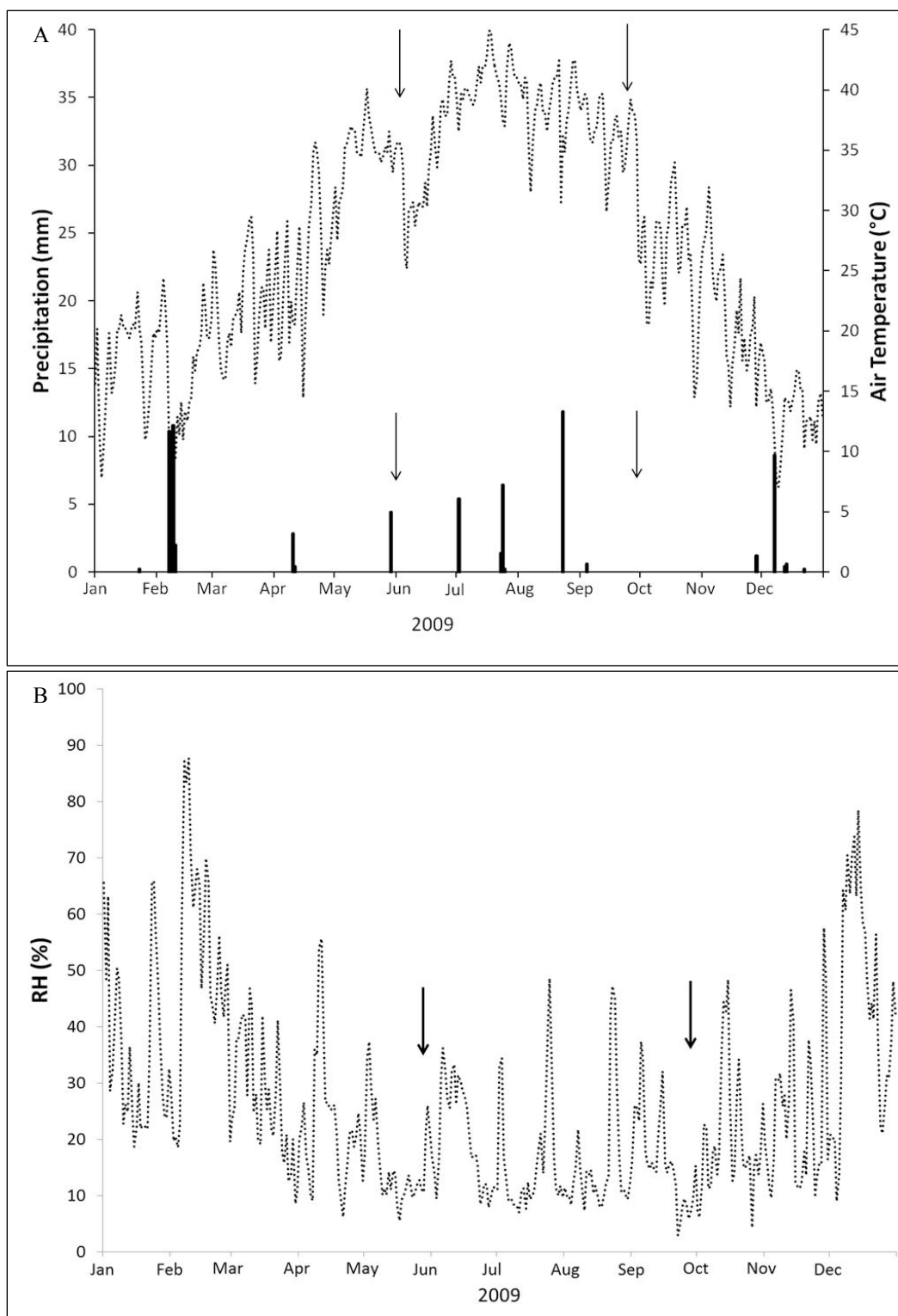
Figure 16. Precipitation (mm) events (solid bars) and daily maximum air temperature (°C) (dotted line) (A) and mean relative humidity (%) (B) in 2009 at the Hayden piedmont, Mojave National Preserve, CA. Arrows indicate the start and end of the simulated wash flow experiment and sampling period (Jun – Sep).

<u>Experimental Design</u>

The study site was carefully selected based on soil substrate, a large enough number of plants within 5 m of both sides of the wash, no other washes within at least 5 m from sampled plants, and no signs of recent disturbance. A 30 m stretch of a 1 m wide wash was selected for experimental addition of water. Within 5 m of each side of the wash, equal numbers of *Larrea* (n = 28; 14 per side) and *Ambrosia* (n = 36; 18 per side) plants were selected and their minimum distance from a wash edge was recorded. The amount of water supplied to the wash during the experimental pulse was calculated to fill a subsurface area based on a trapezoid cross-sectional area (Fig. 19) under the assumption that there would be some lateral movement of water as it infiltrated to depth,

$$(a + b)/2 * h = \text{area wetted zone} \qquad \qquad \text{(Eq. 4)}$$

where a = wash width (1 m); b = width at the base of the wetted zone (2 m), assuming that water spreads laterally in a proportion of 1/2 the depth, and h = wash depth or height (1 m) (equation 4). The cross-sectional area of the wetted zone (1.5 m^2) multiplied by the desired wetted wash length (30 m) resulted in the volume needed to fill the wash (45 m^3). The product of the desired volume of water and the soil water holding capacity (200 L/m^3) (based on soil porosity of 0.2%) resulted in a total of 9000 L (2377 gal) of water needed to saturate the desired volume.
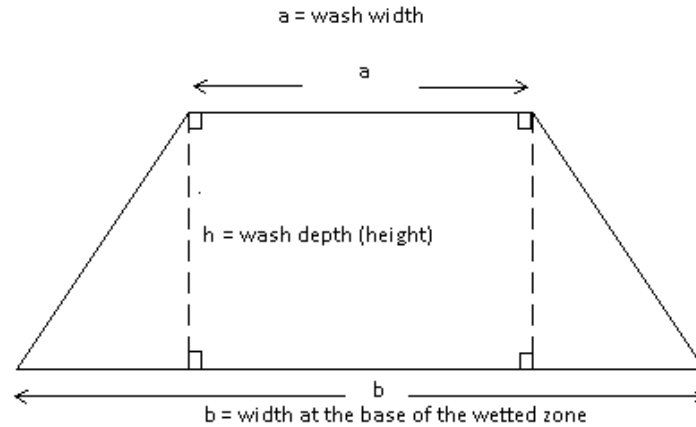
a = wash width

Figure 17. Representation of how water is assumed to infiltrate into the wash. Water input into a wash of width (a) is assumed to spread laterally in a proportion of ½ the desired wetted depth (h), expanding the width at the base of the wetted area (b) resulting in the total cross-sectional area to be wetted.

Using a mass-balance approach, I estimated the type of natural summer event that my water pulse simulated. My assumptions were: (1) reaching the wash has 100% infiltration and any water running out of the channel from the bottom is replaced by an equal amount coming from the top of the channel, and (2) runoff from adjacent non-wash surfaces up to 3 m generates 75% runoff into the wash (from both sides of the wash). With these estimated, I calculate that my event represents approximately a 46 mm event. That is,

$$\text{Infiltration Water} = x * \big((0.75 * \text{interfluvial area}) + \text{wash area}\big) \qquad \text{(Eq. 5)}$$

where the unknown value x = precipitation event size (m), infiltration water = amount of water poured into the wash (7.575 m^3), interfluvial area = distance from both sides of the wash that plants responded [i.e., 2 sides * 3 m wide/side * 30 m (wash length)], and wash area = 1 m * 30 m (i.e., wash width * wash length).

The experiment was conducted in summer 2009 and consisted of one large watering event on June 2 followed by periodic sampling over the subsequent 17 weeks.

A 'pulse' of water was released from a 2000 gallon water truck directly into the wash along a 30 m stretch. Water was dispersed throughout the 30-m wash section using a series of connected fire hoses (8 cm diameter) that were perforated with two 6 mm holes (on opposite sides of the hose) every 25 cm along the 30 m stretch. This allowed uniform water distribution to the wash at a rate of approx. 42 to 63 L/min. Following the water pulse a cross-sectional trench was dug at both ends of the wash to examine the dispersion of water in the soil profile. The water was found to penetrate to a depth of one meter at both ends of the wash and the wetted area width was ca. 2 m, confirming our assumption of some lateral water spread.

Sampling and Measurements

Before and after the pulse event, three physiological measurements were taken. They included, pre-dawn and mid-day xylem water potential (Ψ_x) which are measures of minimum and maximum daily plant water stress, respectively, and leaf stomatal conductance (g_s), a measure of active water release from the plant (stomatal conductance is also related to leaf uptake of carbon dioxide for photosynthesis). At the start of the experiment *Ambrosia*, a small drought-deciduous shrub, was at the onset of summer dormancy resulting in very limited leaf material available for sampling. To avoid significant damage to *Ambrosia* plants over the duration of the experiment, the 36 individuals were divided into two equal subsets of 18 plants (nine per side) for sampling on alternate days. *Larrea* plants were large enough that sampling was not expected to significantly damage any individuals. All physiological measurements were taken one day before the pulse (Jun 1) to serve as a baseline (Day -1), and then again following the

pulse on days 1 (Jun 5), 3 (Jun 5), 6 (Jun 8), 13 (Jun 15), 21 (Jun 23), 35 (Jul 7), 78 (Aug 19) and 119 (Sept 29).

Water Potential and Conductance Sampling. Values of xylem water potential were measured in the field with a Scholander-type pressure chamber (Model 1000, PMS Instrument Company, Albany, OR, USA). Two to three stem water potential measurements per plant were taken at pre-dawn (Ψ_{pd}) between the hours of 2:30 and 4:30 a.m., and at mid-day (Ψ_{md}) between the hours of 12:30 and 2:30 p.m., Pacific Daylight Standard Time (PDT). Stems containing live leaves were cut, immediately placed into plastic bags and the bag was sealed to avoid desiccation of the cut branch prior to measuring with the pressure chamber. All samples were measured within 10 min of being cut. Water potential measurements were taken on 24 of the 28 *Larrea* plants (12 per side) and on 36 *Ambrosia* plants, but as subsets of 18 per day (as described above). Stomatal conductance measurements were taken on all 28 *Larrea* plants. All 36 *Ambrosia* plants were also measured during each sampling period, except in late summer when most *Ambrosia* plants entered dormancy and there were no leaves available for sampling. Stomatal conductance measurements were done using a hand held leaf porometer (Decagon Devices, Inc., Pullman, WA, USA) between 8:30 a.m. and 12:00 p.m., PDT.

Data Analysis

All statistical analyses were performed using SAS 9.0 software. An alpha level of 0.05 was used for all statistical tests unless otherwise noted. The experiment is a two factor, mixed effects, repeated measures design, thus a mixed model repeated measures analysis was used (SAS procedure MIXED) to analyze the watering treatment effect on

each of the dependent variables: Ψ_{pd}, Ψ_{md}, and g_s. Mixed models should be used when one has both random and fixed effects. Species (between-subjects factor), day (within-subjects factor) and their interaction were modeled as fixed effects, with day as the repeated measure, while individual plants were modeled as random effects. Distance from wash was a subject-dependent predictor variable and used as a covariate in the model.

When using the REPEATED statement in PROC MIXED the default covariance structure that SAS uses assumes that the repeated measures are of equal variance and are independent of each other, or uncorrelated. Since the repeated measures are in fact correlated, a different covariance structure was specified. The covariance structure that best fits the data is the autoregressive order 1 covariance, denoted as AR(1). However, AR(1) requires that observations are equally spaced over time, which is not the case with this study design. As such, a time-series covariance structure in which the correlations decline as a function of time (the spatial power law) was used because this provides a direct generalization of the AR(1) structure treating unequally spaced data as a spatial process in one dimension (Littell et al. 1996).

Multiple Comparisons. To determine the effect of distance-from-wash on the response variables Ψ_{pd}, Ψ_{md}, and g_s, distance (continuous data) was categorized into three intervals (categorical data). The distance categories are as follows: 0-1 m - plants bordering the wash; 1-3 m - plants at an intermediate distance from the wash; 3-5 m - plants at furthest distance from the wash. Dunnett's test (SAS procedure GLM) is a multiple comparisons procedure in which not all pairwise comparisons are of interest, only those used to compare several treatments against a control (Dunnett 1955).

Dunnett's test was performed to compare the group (distance category) means each post-pulse day against the baseline pre-pulse value (day -1) for both *Larrea* and *Ambrosia*.

Stomatal Conductance Analysis by Day. Stomatal conductance can be strongly influenced by short-term environmental factors such as air temperature, relative humidity, and leaf-to-air vapor pressure deficit (VPD) (Yan et al. 2000). As such, differences among the three distance categories within each day were used to examine variation in response to the pulse for each species (Tukey's multiple comparisons test). The Bonferroni correction, α / n, where α is the desired significance level, was applied to account for the number of comparisons being performed, which in this case was three $(0.05 / 3 = 0.0167)$. Therefore, a more conservative significance level ($P < 0.01$) was used to determine statistically significant differences among the three distance categories. *Ambrosia* plants 3-5 m from the wash were dormant by day 78 and therefore days 78 and 119 were excluded from this analysis.

<div align="center">Results</div>

Overall Treatment Effects

Day and distance from wash had a significant effect on Ψ_{pd}, Ψ_{md}, and g_s responses to the pulse of water (Table 3). The significant day effect may not be surprising due the duration of the experiment (119 days following the pulse), which was purposely done to see how long the pulse effect lasted and values returned to pre-pulse conditions. The significant distance-from-wash effect was also expected since my goal was to quantify wash effect on two morphologically distinct shrubs as a function of distance from the wash margin.

Larrea and *Ambrosia* (species effect) were different in terms of Ψ_{pd} (df = 1, 57; f

= 6.93; P = 0.01) and g_s (df = 1, 61; f = 28.28; P < 0.0001), irrespective of day and

distance from wash, but no species differences were detected for Ψ_{md} (df = 1, 57; f =

0.06; P = 0.81), signifying that both species exhibited similar minimum water potentials

(Table 3).

The species-by-day interaction was not significant for Ψ_{pd} (df = 8, 293, f = 0.73; P

= 0.67) and Ψ_{md} (df = 8, 289; f = 1.4; P = 0.20) (Table 3), indicating that *Larrea* and

Ambrosia had similar water potential patterns after the pulse. However, there was a

significant species-by-day interaction for g_s (df = 8, 445, f = 8.31; P < 0.0001), probably

due to different phenologies between species creating differing rates of carbon uptake and

water release over the course of the experiment.

Table 3. Mixed model results for effects of species, day, species-by-day, and distance on three physiological parameters following the wash water pulse: pre-dawn water potential (Ψ_{pd}), mid-day water potential (Ψ_{md}), and stomatal conductance (g_s). F-statistics are reported, accompanied by significance levels (* $P \leq 0.05$, ** $P < 0.0001$).

	Species	Day	Species-by-Day	Distance
Ψ_{pd} (MPa)	6.93*	44.00**	0.73	297.24**
Ψ_{md} (MPa)	0.06	49.97**	1.40	306.52**
g_s (mmol m^{-2} s^{-1})	28.28**	21.12**	8.31**	82.51**

Plant Water Status

Plant water status of *Larrea* and *Ambrosia* individuals prior to the start of the

experiment indicated very dry conditions (Ψ_{pd} ranged from -4.9 to -6.6 MPa; Ψ_{md} ranged

from -6.1 to -7.2 MPa). Three days prior to day -1 (pre-pulse) a 4.4 mm rainfall event

took place, but this size of event has been deemed insufficient to stimulate perennial plant activity and thus should not have affected pre-pulse measurements of Ψ_{pd} and Ψ_{md}.

Pre-Dawn Water Potentials. Based on Dunnett's tests, Ψ_{pd} values became significantly greater than pre-pulse (Day -1) values as early as day 1 for *Larrea* plants located 0-1 m from the wash. The Ψ_{pd} values peaked on day 13, and remained significantly greater than pre-pulse values through day 78, even though they drastically declined after day 35 (df = 8; f = 213.25; $P < 0.0001$) (Fig. 20). *Larrea* plants 1-3 m from the wash showed a similar trend of increasing Ψ_{pd} immediately after the pulse and declining dramatically after day 35, but significant differences from pre-pulse values occurred only on days 6, 13, and 21 during which Ψ_{pd} means were essentially the same (-2.86, -2.86, and -2.84 MPa, respectively) (df = 8; f = 4.06; $P = 0.0016$) (Fig. 20). *Larrea* plants 3-5 m from the wash did not have significantly higher Ψ_{pd} on any days, and exhibited significantly lower Ψ_{pd} than pre-pulse values on day 119 (df = 8; f = 4.14; $P = 0.0004$) (Fig. 20) with the lowest recorded mean Ψ_{pd} (-6.82 MPa) for *Larrea* throughout the entire experiment.

For *Ambrosia*, Ψ_{pd} values that were significantly greater than those pre-pulse (Day -1) first appeared on day 1 for plants 0-1 m from the wash and remained significantly greater through day 78. On day 119, Ψ_{pd} values were significantly lower than the pre-pulse values (df = 8; f = 160.5; $P < 0.0001$) (Fig. 20). *Ambrosia* plants 1-3 m from the wash exhibited Ψ_{pd} values that appeared higher than those pre-pulse on days 1 through 35; however, day 13 was the only day that was significantly greater (df = 8; f = 3.67; $P = 0.0019$) (Fig. 20). There was no one distinct peak in maximum Ψ_{pd} for *Ambrosia* plants up to 3 m from the wash, possibly due to two sets of plants measured on

alternate days, although, the trends for *Ambrosia* at 1-3 m were similar to those of

Larrea, with values declining after day 35. Predawn Ψ of *Ambrosia* plants 3-5 m from

the wash did not depart from pre-pulse values through day 35, but were significantly

lower on day 78, for which its lowest mean Ψ_{pd} value of -6.76 MPa was recorded (df = 7;

f = 3.56; *P* = 0.0047) (Fig. 20). By day 119, *Ambrosia* plants 3-5 m from the wash were

fully deciduous.

Figure 18. Pre-dawn water potential (Ψ_{pd}) following simulated wash flow for *Larrea tridentata* (closed symbols) and *Ambrosia dumosa* (open symbols) plants at different distances from the wash (mean ± SE) across all days sampled. Symbols indicate significantly greater (*) and lower (†) group (species, distance category) means on that day from that of pre-pulse (day -1) values ($P \leq 0.05$).

Mid-Day Water Potentials. Similar to Ψ_{pd} responses, Ψ_{md} values were

significantly higher as early as one day following the wash pulse for both *Larrea* and

Ambrosia plants 0-1 m from the wash. However, this effect only lasted through day 35 in comparison to the pulse effect on Ψ_{pd} that lasted through day 78. By day 119, *Larrea* had significantly lower Ψ_{md} values than those pre-pulse (*Larrea* df = 8; f = 147.07; $P <$ 0.0001; *Ambrosia* df = 8; f = 103.23; $P < 0.0001$) (Fig. 21). *Larrea* and *Ambrosia* plants 1-3 m from the wash responded with significantly higher Ψ_{md} values than those pre-pulse on days 3, 6, 13, and 21 (*Larrea* df = 8; f = 6.53; $P < 0.0001$; *Ambrosia* df = 8; f = 5.15; $P < 0.0001$) (Fig. 21), while *Larrea* and *Ambrosia* plants 3-5 m from the wash did not exhibit an increase in Ψ_{md} from pre-pulse, but had significantly lower values on day 119 for *Larrea* (df = 8; f = 4.4; $P = 0.0002$) and day 78 for *Ambrosia* (df = 7; f = 5.71; $P =$ 0.0002) (Fig. 21). This was the same pattern shown for Ψ_{pd}, indicating that plants of *Larrea* and *Ambrosia* farther than 3 m from the wash margin did not respond to the pulse of wash water.

Stomatal Conductance

Pulse-water uptake resulted in an increase of g_s for both *Larrea* and *Ambrosia*; however, the two species exhibited contrasting g_s response patterns. *Larrea* plants 0-1 m and 1-3 m from the wash showed a marked increase in g_s three days following the pulse. Stomatal conductance peaked on that day and declined thereafter, with g_s values back to pre-pulse values by day 21 (0-1 m df = 8; f = 24.83; $P < 0.0001$; 1-3 m df = 8; f = 13.22; $P < 0.0001$) (Fig. 22). *Larrea* plants 3-5 m from the wash did not show a change in g_s following the pulse of wash water, and actually had significantly lower g_s values on days 78 and 119 (df = 8; f = 6.46; $P < 0.0001$) (Fig. 22).
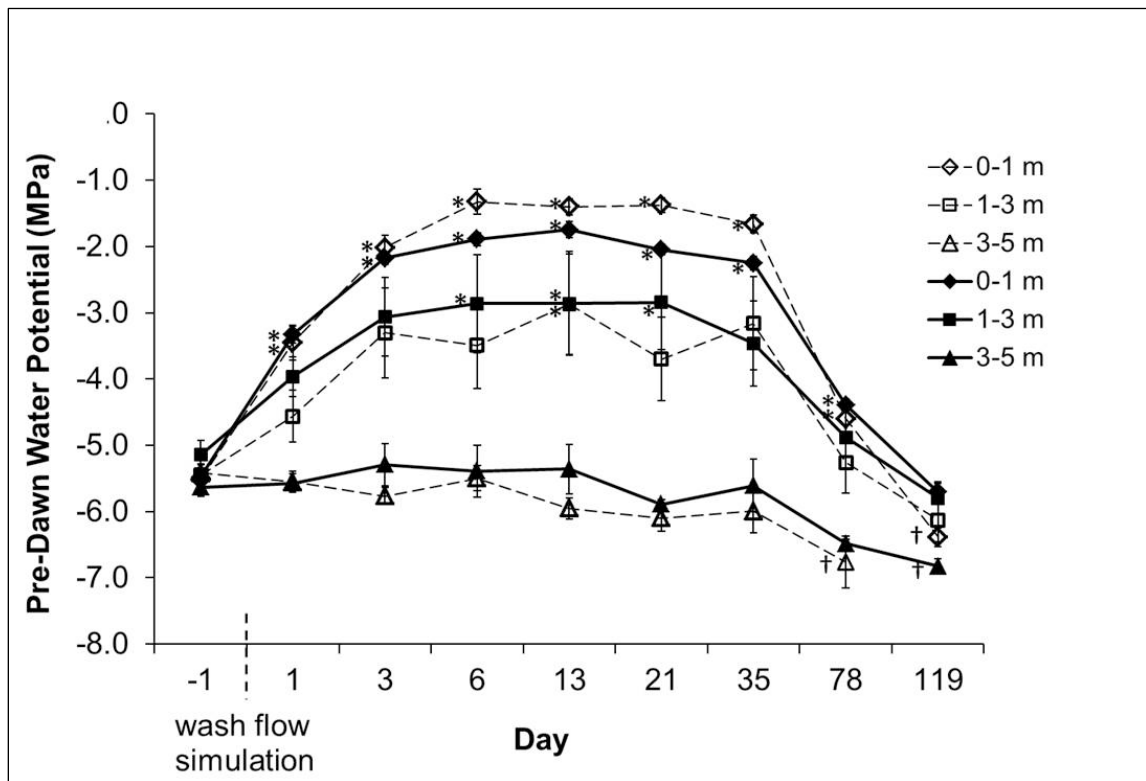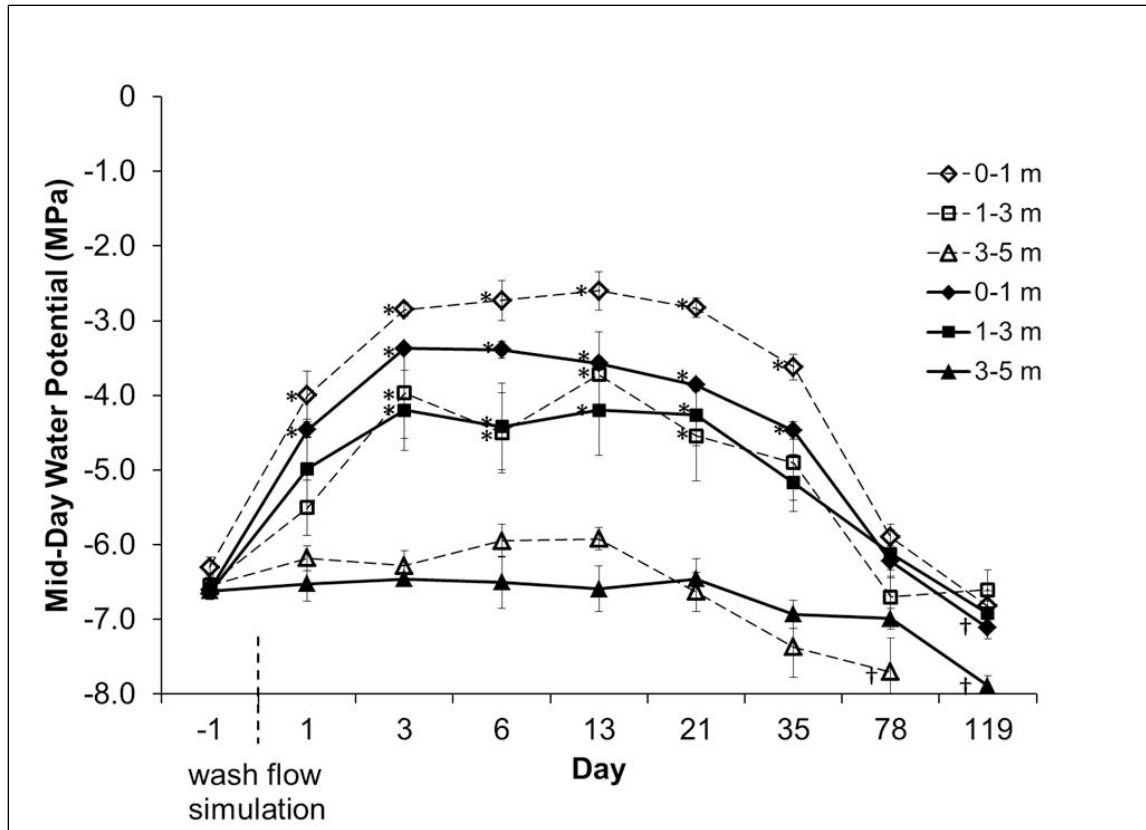
Figure 19. Mid-day water potential (Ψ_{md}) following simulated wash flow for *Larrea tridentata* (closed symbols) and *Ambrosia dumosa* (open symbols) plants at different distances from the wash (mean ± SE) across all days sampled. Symbols indicate significantly greater (*) and lower (†) group (species, distance category) means on that day from that of pre-pulse (Day -1) values ($P \leq 0.05$).

All *Ambrosia* plants (even those > 3 m) showed significant increases of g_s from pre-pulse values on day 6. Plants > 3 m from the wash never again had g_s values greater than those pre-pulse, but at distances < 3 m, g_s continued to increase through day 21 and remained greater than day -1 through day 35. By day 78, plants at all distances from the wash had g_s values no different than those of pre-pulse (0-1 m df = 8; f = 18.41; $P <$ 0.0001; 1-3 m df = 8; f = 5.89; $P < 0.0001$; 3-5 m df = 6; f = 3.95; $P = 0.0019$) (Fig. 22).

Daily Stomatal Conductance. Pre-dawn and mid-day water potentials indicated that no plants, *Larrea* or *Ambrosia*, farther than 3 m from the wash took up water from the pulse; however, both species showed a slight increase in stomatal conductance 3-6

days following the pulse, with *Ambrosia* exhibiting significantly greater g_s on day 6. This indicates that for plants further than 3 m from the wash greater g_s was not a result of improved water status from the pulse of water, but was probably influenced by other abiotic factors in the environment. To examine the effect of possible environmental influences on stomatal conductance responses, differences among the three distance
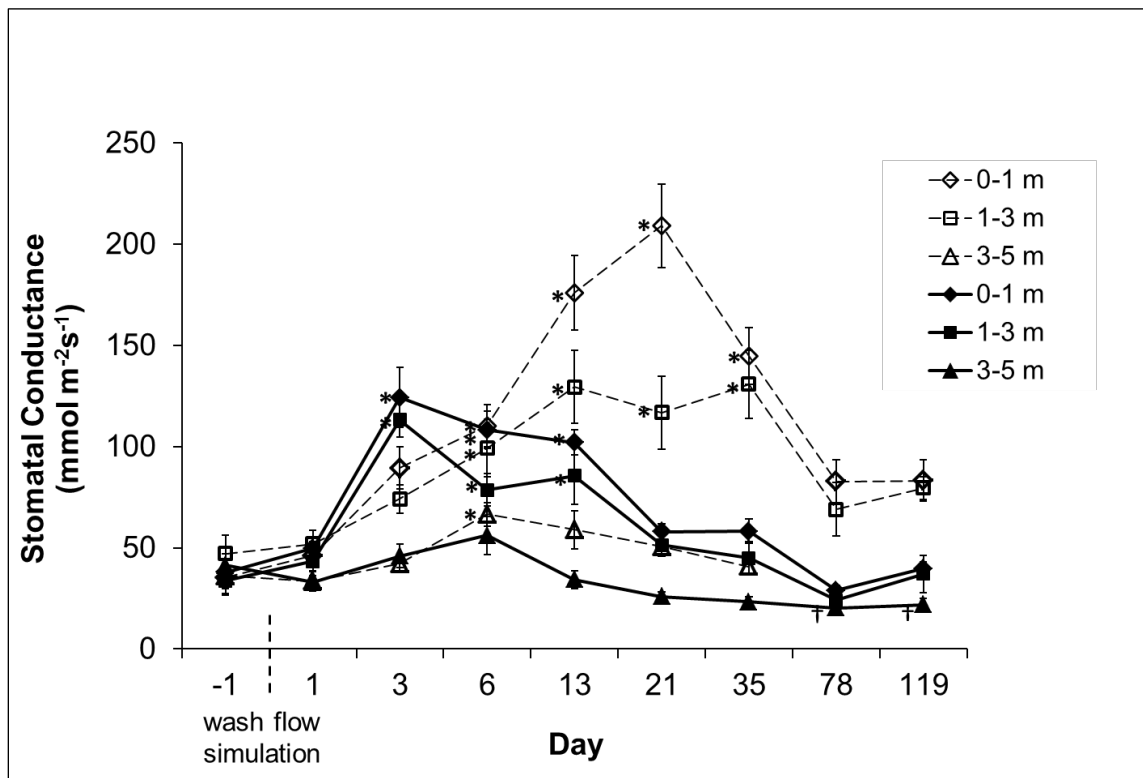
Figure 20. Stomatal conductance (g_s) values following simulated wash flow for *Larrea tridentata* (closed symbols) and *Ambrosia dumosa* (open symbols) plants at three distances from the wash (mean ± SE) across all days sampled. Symbols indicate significantly greater (*) and lower (†) group (species, distance category) means on that day from that of pre-pulse (Day -1) values ($P \leq 0.05$).

categories were compared within each day. There were no significant differences of stomatal conductances among the three distance categories on day -1 for both *Larrea* (df = 2; f = 0.57; P = 0.5744) and *Ambrosia* (df = 2; f = 0.53; P = 0.5926). On day 1 *Larrea*

plants within 1 m of the wash had significantly greater g_s than those furthest from the

wash (3-5 m) (df = 2; f = 5.98; P = 0.0075). This same trend occurred on day 6 (df = 2; f

= 8.85; P = 0.0012) and on day 35 (df = 2; f = 11.44; P = 0.0003) for *Larrea*. On days 3

(df = 2; f = 13.27; P = 0.0001), 13 (df = 2; f = 25.12; P < 0.0001), and 21 (df = 2; f =

23.73; P < 0.0001) *Larrea* plants 0-1 m and 1-3 m from the wash had significantly

greater g_s than those 3-5 m from the wash; however, plants 0-1 m away were not

significantly different from those 1-3 m from the wash on those days. There were no

significant differences of g_s among groups on days 78 and 119 for *Larrea*.

   Ambrosia plants revealed quite a different pattern as plants further than three

meters from the wash had similar g_s values as those plants 0-1 m and 1-3 m from the

wash on days 1 (df = 2, f = 2.72, P = 0.08) and 6 (df = 2, f = 3.51, P = 0.04). In contrast,

plants greater than three meters from the wash had significantly lower g_s than plants at

both 0-1 m and 1-3 m from the wash on days 3 (df = 2; f = 10.36; P = 0.0004), 13 (df = 2;

f = 12.55; P < 0.0001) and 35 (df = 2; f = 17.55; P < 0.0001). On day 21 plants in all

three distance categories were significantly different from each other (df = 2; f = 21.27; P

< 0.0001). All daily stomatal conductance results are summarized in Table 4.

Table 4. Tukey's all pairwise comparisons of mean g_s among all distance categories within each day pre- (Day -1) and post- (Days 1-119) application of pulse water. * denotes a significant difference at the $P < 0.01$ level, and NS indicates a non-significant result.

Distance from wash	*Larrea tridentata*			*Ambrosia dumosa*		
	0-1 m vs. 1-3 m	1-3 m vs. 3-5 m	0-1 m vs. 3-5 m	0-1 m vs. 1-3 m	1-3 m vs. 3-5 m	0-1 m vs. 3-5 m
Day -1	NS	NS	NS	NS	NS	NS
Day 1	NS	NS	*	NS	NS	NS
Day 3	NS	*	*	NS	*	*
Day 6	NS	NS	*	NS	NS	NS
Day 13	NS	*	*	NS	*	*
Day 21	NS	*	*	*	*	*
Day 35	NS	NS	*	NS	*	*
Day 78	NS	NS	NS	No Data	No Data	No Data
Day 119	NS	NS	NS	No Data	No Data	No Data

Discussion

Previous studies of desert shrub responses to summer precipitation have only examined how surface water, penetrating the top soil layers (< 50 cm), affected perennial vegetation (Barker et al. 2005; BassiriRad et al. 1999; Lin et al. 1996; Ogle and Reynolds 2002; Schwinning et al. 2002; Schwinning et al. 2003; Snyder et al. 2004), but in my system, rain generated from high intensity, short duration summer monsoons rarely infiltrates into deeper soil layers (> 50 cm) on inter-wash surfaces (Miller et al. 2009). Furthermore, hot soil temperatures, and thus high evaporation, may limit the capacity of perennial plants to take up water from the uppermost soil layers (BassiriRad et al. 1999; Lin et al. 1996).   Unlike other studies, I examined a simulated summer precipitation event that would result from substantial runoff into washes, and subsequent water

penetration to a depth of 1 m in that wash.   I found that positive physiological responses by both *Larrea* and *Ambrosia* lasted for at least one month following the pulse, even when plants are up to 3 m away from the wash. My results suggest that wash properties, such as high infiltration rates and additional water due to runoff from adjacent surfaces, may provide a potentially valuable summer water source in deeper soil layers, at least temporarily, for perennial shrubs along wash margins in the Mojave Desert.

Many studies have examined longer-term effects of summer precipitation on desert shrub physiology and how these responses vary within a community (Barker et al. 2005; Franco et al. 1994; Naumberg et al. 2003; Ogle and Reynolds 2002; Schwinning et al. 2002; Snyder et al. 2004), but a complete understanding of the significance of summer precipitation in desert systems must also include short-term plant responses both within and among species. The few studies that have focused on short-term responses suggest that the greatest increase in plant activity occurs within the first week following summer rainfall and that there is substantial variation among species (Barker et al. 2005; BassiriRad et al. 1999; Lin et al. 1996; Schwinning et al. 2002; Schwinning et al. 2003). Differential short-term water use patterns in response to summer pulses have the potential to alter competitive interactions among species, and thus community structure in the long-term, especially under scenarios of increasing summer precipitation in the Mojave Desert (Ehleringer et al. 1991; Ogle and Reynolds 2004; Schwinning and Ehleringer 2001; Schwinning et al. 2002; Snyder et al. 2004).

My results indicate that both *Larrea* and *Ambrosia* experienced significant increases in Ψ_{pd}, Ψ_{md}, and g_s within the first few days following the pulse; however responses were markedly different between species (Figs. 20, 21 and 22). This

dissimilarity was expected based on differences in leaf phenology (evergreen vs. drought-deciduous), physiology (drought tolerant vs. drought avoider), and morphology (deeper rooted vs. shallower rooted) — traits that have been attributed to differential responses to summer precipitation among plant functional groups, although other traits may also play a role (Ehleringer et al. 1991; Lin et al. 1999; Ogle and Reynolds 2004; Schwinning and Ehleringer 2001; Schwinning et al. 2002; Schwinning et al. 2003).

Short-Term Physiological Responses to Summer Precipitation

Short-term responses to summer precipitation have been found to vary among species in other desert systems. For example, in the Colorado Plateau desert, *Artemesia filifolia* did not exhibit significant increases in water potential (Lin et al. 1996) or gas exchange rates (Schwinning et al. 2002) immediately following simulated summer precipitation events $\geq$ 20 mm, while *Coleogyne ramosissima* experienced significant improvements in both water potential (Lin et al. 1996) and gas exchange rates (Schwinning et al. 2002). Additionally, *Gutierrezia sarothrae*, a shrub with both lateral and deep roots, increased Ψ_{pd} in response to a 19 mm event just 1 day after watering, while *Ceratoides lanata*, a deeply rooted woody shrub, was unresponsive to the event (Schwinning et al. 2003). These differences were largely attributed to soil water resources being accessed from varying depths among species (i.e., soil water partitioning).

In my study, the rapid and extensive response of *Larrea* is not surprising, as *Larrea* has been found to respond quickly to summer precipitation events in a number of other studies, possibly due to persistence of leaves and summer activity allowed by access to deep soil water (Franco et al. 1994), and the ability of *Larrea* to maintain active

roots in relatively dry soils (Wilcox et al. 2004). In the Chihuahuan Desert, where

summer precipitation is dominant, short-term improvements of water status and stomatal

conductance in *Larrea* were observed three days following a simulated precipitation

event of 30 mm (BassiriRad et al. 1999), and two days following a 23 mm event (Yan et

al. 2000). In the Mojave Desert, Barker et al. (2005) found that *Larrea* experienced

significant increases in Ψ_{pd} and g_s one week after a simulated 25 mm summer

precipitation event that followed another 25 mm event four weeks prior. The Ψ_{pd} values

remained higher than pre-pulse over one month following two additional pulses, but g_s

dropped over this period and approached pre-pulse values (Barker et al. 2005).

My results for *Larrea* within 3 m from the wash were similar to those of Barker et

al. (2005) showing that by day 35, Ψ_{pd} were still high, but g_s values had returned to pre-

pulse levels (Fig. 20). Barker et al. (2005) did not measure responses within the first

week following the watering treatments, although the increase in Ψ_{pd} (ca. 3.5 MPa) one

week after a watering treatment was similar to that seen after six days in my study.

Additionally, peak Ψ_{pd} values in my study were similar to those reported by Fonteyn and

Mahall (1981) for *Larrea* following a 60 mm summer event. These results indicate that

large summer precipitation events (20 – 60 mm) in the Mojave Desert facilitate rapid

physiological responses in *Larrea* and demonstrate that *Larrea* has pronounced strong

stomatal regulation even at high water potentials (i.e., low water stress), which may

facilitate greater efficiency of water use during photosynthetically active periods (Franco

et al. 1994; Yan et al. 2000).

The response exhibited by *Ambrosia* could be attributed to its physiological status

at the start of the experiment as *Ambrosia* plants had not yet become fully summer

dormant (evident by the presence of minute, but live leaves on the plant), suggesting that active roots were still present in the soil and available for water uptake. Since *Ambrosia dumosa* has been found to increase fine-root production when soil water is available (Wilcox et al. 2004), it is possible that a 4.4 mm rain event three days prior to the first measurements could have initiated some root growth and subsequently led to enhanced rates of water uptake after the wash pulse (Schwinning et al. 2002). However, there is little evidence that a 4.4 mm rain event, especially in summer, could stimulate the growth of new roots and facilitate subsequent activity (Beatley 1974). In addition, despite an immediate improvement of plant water status by *Ambrosia*, there was a delay in g_s until day 21 when responses were then maximized, indicating that post-pulse growth did limit an earlier response by *Ambrosia* to some degree.

The results for *Ambrosia* are valuable, as there is limited information regarding this species' response to summer precipitation. In the few studies of this species, however, *Ambrosia* has been found to respond to large summer rain events in the Mojave Desert. For example, water potentials exceeded -1.0 MPa following a 60-mm event (Fonteyn and Mahall 1981), and Naumberg et al. (2003) found that (under elevated CO_2) *Ambrosia dumosa* increased g_s following summer monsoon events, but only in a year that experienced above-average cool season precipitation prior to the summer monsoon period. In the current study, cool season precipitation (Oct – April) during the 2008/2009 hydrologic-year was low, 75.6 mm, and well below the average reported for this region of the Mojave Desert (95 mm) (Hereford et al. 2006), thus the pulse response of *Ambrosia* I observed cannot be explained solely by precipitation preceding the

experiment. It is likely that plants remained active due, in part, to enhanced soil moisture derived from water runoff into washes (Schwinning et al. 2011; Smith et al. 1997).

Distance-from-Wash Effects on Water Status of Desert Shrubs

Larrea and *Ambrosia* plants 0-1 m and 1-3 m from the wash margin responded to the pulse of wash water with higher Ψ_{pd} and Ψ_{md} (Figs. 20 and 21). There were no significant increases in water potentials for plants further than 3 m from the wash (Figs. 20 and 21). Therefore, to assess wash effects on water status of *Larrea* and *Ambrosia* only those plants 0-1 m and 1-3 m from the wash will be discussed.

Responses of Plants 0-1 m from the Wash. My findings indicate that *Larrea* and *Ambrosia* within one meter of the wash are both capable of rapid water potential responses to summer pulses in the Mojave Desert. Both species had an immediate increase in Ψ_{pd} and Ψ_{md} one day following the pulse, and these responses persisted for over a month (Figs. 20 and 21). Individual Ψ_{pd} responses of *Ambrosia* on days 6 and 13 (representing alternate sets of plants sampled), and of *Larrea* on day 13 indicate that all plants 0-1 m from the wash took up pulse water and responded with higher Ψ_{pd} (Fig. 23). This response is not surprising since lateral root extensions of at least 1 m have been reported for both species (Brisson and Reynolds 1994; Cannon 1913; Chew and Chew 1965; Gile et al. 1998; Singh 1978), enabling water uptake under wash sediments by plants within 1 m away from that channel.

Despite similar pre-pulse values, *Ambrosia* attained higher Ψ_{pd} and Ψ_{md} than *Larrea* over the course of the experiment for plants within 1 m of the wash (Figs. 20 and 21). Although not statistically tested, there appears to be a greater response seen by *Ambrosia* relative to *Larrea*. Higher water potentials for *Ambrosia* plants relative to

Larrea plants within 1 m of the wash could be due to a potentially higher root-to-shoot ratio, or rather root-to-leaf area ratio, for *Ambrosia*. Because *Ambrosia* is deciduous, leaf area increase (i.e., transpirational area) lags behind root area at the onset of growth responses, and when water uptake exceeds water loss, water potential is high (Lambers et al. 2006; Schwinning and Ehleringer 2001). While this explanation seems plausible, without further evidence I cannot conclude that higher root-to-shoot ratios for *Ambrosia* contributed to this presumed differential response within 1 m of the wash. Furthermore, reported values of root-to-shoot ratios for both *Larrea* and *Ambrosia* are typically high, which enhances the ability of these species to take up water from summer pulses, especially when they are located close to washes where soil moisture is high (Smith et al. 1997).

Following day 35 there was a notable decline in both Ψ_{pd} and Ψ_{md}, despite values of Ψ_{pd} still being significantly higher than those exhibited on day -1. This difference persisted through day 78 for both species. The magnitude and duration of response exhibited by plants bordering the wash is likely due to access to a water reservoir that has a relatively long residence time in deep soil layers, where evaporation is more limited. Water down to one meter depth mimics winter precipitation input, which has been known to positively affect long-term plant growth and performance (Beatley 1974).

Responses of Plants 1-3 m from the Wash. Plants 1-3 m from the wash exhibited a similar response pattern as those within 1 m from the wash; however, significant increases occurred later for both species (day 6 for *Larrea* Ψ_{pd}, day 13 for *Ambrosia* Ψ_{pd}, and day 3 for Ψ_{md} for both species) (Figs. 20 and 21). Additionally, significant differences from pre-pulse were shorter lived, lasting only through day 21, indicating that

wash water can sustain plants for three weeks up to 3 m away. What could be perceived as a delayed response might just be a function of root interactions between *Larrea* and *Ambrosia* (Mahall and Callaway 1991). It is likely that plants closest to the wash have more root biomass to exploit soil moisture quickly compared to plants 1-3 m from the wash, in which root growth under wash sediments may be inhibited by neighboring root systems. Inter- and intra-specific root interactions between *Larrea* and *Ambrosia* will be further explored by looking at individual plant responses (rather than the means), but can only be inferred as I have no direct evidence of this possibility.

A pattern of regular variability from day-to-day was obvious in the means of *Ambrosia* (Fig. 20 and 21), but not for *Larrea*. This could just be an artifact of sampling alternate sets of *Ambrosia* shrubs every other day, which was necessary to avoid heavy defoliation throughout the entire sampling period. Nonetheless, individual Ψ_{pd} responses of *Ambrosia* on days 6 and 13 (representing alternate sets of plants sampled), and of *Larrea* on day 13 indicate that not all plants 1-3 m from the wash responded to the pulse of water, (this is also seen in the larger variances of Ψ_{pd}) (Fig. 23). One *Larrea* plant 1-3 m from the wash did not respond while all others did, but six *Ambrosia* plants 1-3 m did not respond, and eight others had an intermediate response (Fig. 23). Taking a closer look at the individual Ψ_{pd} responses of *Ambrosia* plants on days 6 and 13, the mean Ψ_{pd} values were -3.49 ± 0.64 and -2.87 ± 0.76 MPa, respectively, with an overall mean of -3.18 ± 0.31 MPa. On day 6 (set A) four out of eight sampled plants responded to the pulse, and on day 13 (set B) four out of six plants responded, indicated by $\Psi_{pd} <$ -3.18 ± 0.31 MPa (Fig. 23). Since a greater proportion of plants in set B responded to the pulse
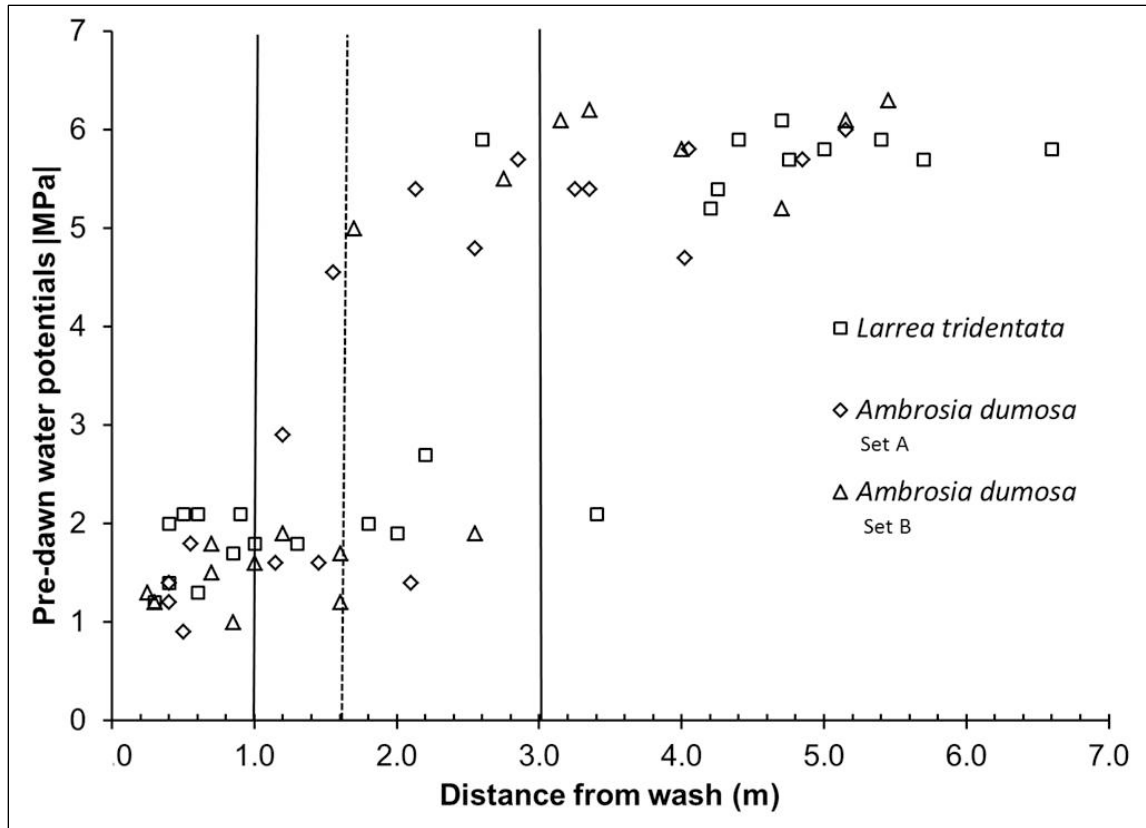
Figure 21. Pre-dawn water potentials (Ψ_{pd}) of *Ambrosia dumosa* on days 6 and 13, and *Larrea tridentata* on day 13, for individual plants plotted vs. distance from the wash. Larger absolute values of Ψ_{pd} indicate more water stressed and no response to pulse, whereas smaller values indicate a positive response leading to less water stress. The solid vertical lines represent a break in the three distance categories (0-1 m; 1-3 m; >3 m). The dashed vertical line represents the maximum lateral root length of 1.6 m reported for *Ambrosia* (Cannon 1913).

of water, the mean Ψ_{pd} for set B was higher than set A (if they were sampled on the same day), causing the alternating pattern observed for *Ambrosia* plants 1-3 m from the wash margin. It appears that there is still some variation in the means between sets A and B of *Ambrosia* plants 0-1 m and 3-5 m from the wash, shown by a subtle alternating pattern between days (Figs. 20 and 21); however, all *Ambrosia* plants 0-1 m from the wash responded to the pulse of water with higher Ψ_{pd} values, while all *Ambrosia* plants 3-5 m from the wash did not respond (Fig. 23), resulting in a smaller difference in the means between sets A and B and thus a more consistent water potential curve across days.

It is not surprising that almost all *Larrea* plants responded up to 3 m from the wash as *Larrea* roots have been found to extend laterally up to twice the distance of its height (Brisson and Reynolds 1994). Studies have found lateral roots extending 2 to 3 m in all directions (Brisson and Reynolds 1994; Cannon 1913; Singh 1978), and even > 4 m (Chew and Chew 1965; Gile et al. 1998). Of all *Larrea* in my study, only one that was within 3 m (at 2.6 m) from the wash did not respond to the pulse with higher Ψ_{pd}. It is possible that root growth was inhibited by two *Larrea* plants growing closer to the wash, as *Larrea* roots have been found to inhibit root growth of other *Larrea* roots nearby (Mahall and Callaway 1991).

On the other hand, while *Ambrosia* has an established lateral root system (Cannon 1913; Fonteyn and Mahall 1981; Jones 1984), 1.6 m has been documented as the maximum lateral root extension for this species (Cannon 1913). Furthermore, dominant lateral roots are most likely found in large plants (> 80 cm canopy diameter) (Jones 1984), of which only one plant 1-3 m from the wash occurred at my study site (average canopy diameter of *Ambrosia* shrubs at the study site were 0.54 m). This plant was, as suggested, found to respond with higher Ψ_{pd}. But in the end, since *Ambrosia* needs to be closer to the wash than *Larrea* for roots to reach below wash sediments and extract water (Schwinning et al. 2011); it is not surprising that some *Ambrosia* plants 1-3 m from the wash did not respond while others did.

Using -3.18 MPa as the cutoff for plant pulse responses on days 6 and 13, roughly half of *Ambrosia* plants 1-3 m from the wash responded while the other half did not (Fig. 23). Six out of seven plants up to 1.6 m from the wash responded, corresponding to the lateral root extension of 1.6 m suggested by Cannon (1913). These plants possibly

concentrate their roots in areas of increased soil moisture such as into washes. However, there was one plant 1.55 m from the wash that did not respond (Fig. 23). It was the smallest *Ambrosia* plant measured in this study (canopy diameter = 0.28 m), and small plants (< 40 cm canopy diameter) have been found to have fewer lateral roots compared to larger plants (Jones 1984). Another possible explanation for the lack of response by some *Ambrosia* in the 1-3 m range is root territoriality of other *Larrea* and/or *Ambrosia* plants that are closer to the wash (Schenk et al. 1999). For the small *Ambrosia* 1.55 m from the wash, two other *Ambrosia* plants were closer to the wash and may have interfered with water uptake by this smaller plant (Mahall and Callaway 1991).

The majority of *Ambrosia* plants > 1.6 m did not respond, with only two exceptions at distances 2.1 and 2.55 m from the wash (Fig. 23). These two plants were located within 1 m of each other and there were no other plants, *Larrea* or *Ambrosia*, along the wash margin that might interfere with water uptake by these plants. Our soil pits confirmed lateral movement of water up to 0.5 m from the physical wash (and wetting) margin, making those plants at 2.1 and 2.55 m from the wash margin functionally only 1.6 and 2.05 m, respectively, from the pulse water. Nonetheless, the responses of these two plants suggest that some *Ambrosia* roots may extend farther than the maximum measured lateral distance of 1.6 m. It is also possible that this circumstance may be specific to *Ambrosia* only when they are concentrated near wash margins where increased water is made available in deeper soil layers.

Utilization of Wash Water by Desert Shrubs

The significant species and day effect on g_s indicates notable physiological differences in the potential uptake of carbon by photosynthesis and release of water by

transpiration between *Larrea* and *Ambrosia* (Table 3). Stomatal conductance (g_s) patterns between species were quite different but for both species plants closest to the wash exhibited the highest g_s responses with declining values farther from the wash, a response that was similar to those patterns observed for water potential (Fig. 22). However, some notable differences between g_s and water potential responses existed. For example, *Ambrosia* plants > 3 m from the wash exhibited significantly higher average g_s values on day 6 compared to pre-pulse values (Fig. 22), and these values were not significantly different from those of plants within 3 m from the wash (Table 4), despite water potential values indicating lower pulse water uptake by the plants > 3 m from the wash. This response is most likely due to environmental conditions, as lower temperatures and higher relative humidity (RH) can increase g_s (Franco et al. 1994; Lambers et al. 2006). Indeed, high daytime temperatures (approx. 35°C) and low RH (16.7% and 9.4%, respectively) during sampling on days -1 and 1 were followed by a 9°C drop and a tripling of RH by day 3 (Fig. 18A, B). Lower temperatures and high RH leading up to day 6 could account for the increase in g_s of *Ambrosia* plants, even for those that did not take up water from the pulse. It appears that *Larrea* plants > 3 m from the wash may have responded in a similar way as shown by a slight but insignificant increase of g_s within this group up to day 6 (Fig. 22). While temperature has been suggested to have little effect on stomatal conductance of *Larrea* (Mooney et al. 1978), higher RH decreases leaf-to-air vapor pressure deficit, which has been shown to increase g_s for *Larrea* (Franco et al. 1994).

In contrast to water potentials, g_s values did not change significantly immediately following the pulse (day 1) (Fig. 22), possibly due to the hot and dry conditions that

persisted from day -1 to day 1, or to a short lag in response in spite of higher water potentials. It appears that both species up to 3 m from the wash had started to increase g_s slightly on day 1, but plants > 3 m showed the opposite pattern. The significant difference in *Larrea* plants within 1 m of the wash vs. those > 3 m on day 1 (Table 4) was very minimal compared to the differences that occurred on day 3 (Fig. 22). Nonetheless, these responses represent an ability of *Larrea* to rapidly respond to available water without having to undergo significant physiological or morphological changes.

Stomatal conductance response of *Ambrosia* initially lagged behind that of *Larrea*, as significant differences from pre-pulse values did not occur until day 6 for *Ambrosia*. Eventually, though, g_s for *Ambrosia* exceeded *Larrea* on days 13, 21 and 35. The delayed response exhibited by *Ambrosia* is most likely due to the differences in leaf phenologies between these species whereby *Ambrosia*, like other drought-deciduous shrubs, is constrained early-on by the lack of leaf area (Franco et al. 1994; Lambers et al. 2006). After new leaves are produced, however, drought deciduous shrubs like *Ambrosia* typically exhibit greater activity leading to higher growth rates and more rapid water use than evergreen shrubs such as *Larrea* (Smith et al. 1997). These results indicate some degree of resource-use partitioning among differing plant functional types, in that these two species have differing temporal responses to a summer rain pulse (Ogle and Reynolds 2004). Resource-use partitioning among plant functional types is more often documented as spatial partitioning following winter rains, in which water distribution is more uniform through the soil profile (Schwinning et al. 2002). Nevertheless, summer rains that generate large runoff events as seen in this study may result in similar spatial partitioning in addition to the temporal separation observed.

Growth and Phenology

I also observed physical signs of short-term pulse responses, as plants adjacent to the wash were noticeably greener by day 6 than those further from the wash. *Larrea* had broader, greener leaves with flower buds on some plants by day 13, and *Ambrosia* had new leaves in large numbers on plants near the wash (pers. obs.). Whether or not this input of summer rain translates into a growth advantage for plants near washes could not be determined, as this was not directly addressed in this study. Nonetheless, washes have been found to have a positive impact on the size of *Larrea* and *Ambrosia* plants within 3 m of their margins in the Mojave Desert (Schwinning et al. 2011). Furthermore, Barker et al. (2005) found that increased summer precipitation events in the Mojave Desert led to enhanced photosynthesis the following spring and hence increased net primary productivity. These concordant results suggest that summer rain events have a pronounced, but possibly underappreciated effect on plant growth, root:shoot ratios, and rooting distributions of the two co-dominant plants of this arid ecosystem.

Influence of Increased Summer Precipitation Events in the Mojave Desert

Following the simulated wash flow event, most plants bordering and up to 3 m from the pulsed wash became significantly less water stressed and more physiologically active. However, differences between *Larrea* and *Ambrosia* exist both spatially, in that water uptake is dependent on root morphology, and temporally as leaf phenology dictates the timing of g_s response and thus carbon uptake for photosynthesis.

What constitutes a sufficient amount of moisture to trigger a physiological response? The threshold-delay (T-D) model of Ogle and Reynolds (2004) incorporates lower and upper thresholds on the size of a precipitation pulse that will trigger a plant

response and how these thresholds vary based on plant functional type. The T-D model suggests that shallow-rooted woody plants have a lower precipitation threshold, in that a smaller precipitation event will trigger a response, compared to deep-rooted woody plants (Ogle and Reynolds 2004). While *Ambrosia* has been described as a shallow rooted plant when compared to *Larrea* (Reynolds et al. 2004) both species have been documented to have a dimorphic root system in which shallow lateral roots and deep taproots allow the uptake of water from various depths within the soil profile (Jones 1984; Ogle et al. 2004; Pavlik 2008; Yoder and Nowak 1999). This dimorphic root system can be very advantageous when summer rainfall events cause runoff into washes where the water not only penetrates the top 0.5 m of soil and is available for shallow lateral roots, but also penetrates deeply into the soil profile where it can be used by deeper roots, and may also be stored for longer-term availability.

Typical summer storms in the Mojave Desert can last from 30 - 60 min at intensities of 20 - 60 mm/hr (Miller et al. 2009). These values well exceed the requirement for runoff events (i.e., rates greater than the infiltration capacity), which are generated from high intensity summer storms $\geq$ 0.8 mm/min and lasting longer than 10 – 15 min (David Miller, pers. comm.; Miller et al. 2009). Runoff into washes make small events effectively much larger as more than half of the rain runs off from surrounding surfaces when rainfall is of sufficient intensity and duration (Miller et al. 2009). Even though this simulated event, estimated to be approx. 46 mm, represents a local summer storm of very large intensity for this desert region, a large event upslope could generate a runoff event of this size. Additionally, this demonstrates how even small

summer rain events can have a potentially large impact on vegetation growing alongside washes.

Given that the amount of water supplied in this study exceeds the mean annual summer precipitation in the Mojave Desert, the great response seen by *Larrea* and *Ambrosia* may not be surprising. *Larrea* has been reported to respond to summer events > 25 mm (BassiriRad et al. 1999; Barker et al. 2005; Fonteyn and Mahall 1981; Franco et al. 1994), and *Ambrosia* to events > 20 mm (Fonteyn and Mahall 1981; Naumberg et al. 2003), but *Ambrosia* did not leaf out in response to a 30 mm event in the Mojave Desert that followed a dry winter (Naumberg et al. 2003). How these two species, with contrasting leaf phenologies and physiological adaptations to historically dry summers, will respond to potential increases in summer precipitation in the Mojave Desert will depend largely on the intensity and frequency of such summer events. For example, because *Larrea* remains metabolically active throughout the year, including summer, it may benefit from short pulses of rainfall (Franco et al. 1994), while *Ambrosia* could be negatively affected by such pulses because it may leaf out too early before the onset of the rainy season. This is energetically expensive, and leaves and whole plants may not survive through the dry season (Oechel et al. 1972). However, if several summer rain events occur, *Ambrosia* could greatly benefit, as it has been shown to retain its leaves in the summer with sufficient moisture (Bamberg et al. 1975; David Miller pers. comm.).

Increased summer rain, and thus increased wash flow, also has the potential to affect competitive interactions between *Larrea* and *Ambrosia* in the Mojave Desert. Resource enhancement has been shown to have a positive impact on both species in the short-term, but longer-term effects have indicated that increased wash flow favors the

dominance of *Larrea*, and thus strengthens the competitive advantage of *Larrea* over

Ambrosia (Schwinning et al. 2011). *Larrea* has been viewed as the superior competitor

due to root interactions that inhibit the growth of *Ambrosia* roots nearby (Mahall and

Callaway 1991). Furthermore, because it is drought tolerant, *Larrea* keeps leaves

through dry periods and can respond to summer rain events without the production of

new leaves, unlike *Ambrosia* that must undergo the costly production of new leaves in

response to favorable conditions (Lambers et al. 2006; Smith et al. 1997). However, it

has been suggested that when water is equally available to multiple species, those with

lower WUE, such as *Ambrosia*, should be the better competitor over the species with a

high WUE, such as *Larrea* (Ehleringer and Cooper 1988). This is because *Ambrosia*,

like many other deciduous species, can exhibit very strong exploitation of soil moisture

when it is made available (Schwinning and Hooten 2009), and has relatively high

photosynthetic and growth rates compared to *Larrea* (Smith et al. 1997). The great

response seen by both species in the current study indicate that soil moisture derived from

runoff into washes is readily available to both *Larrea* and *Ambrosia* plants bordering

washes, but does not indicate that this resulted in a competitive advantage of one species

over another.

Plants along washes that experience increased productivity in years with sufficient

moisture derived from runoff may also be negatively affected in years that runoff does

not occur, as they may become reliant on this input of wash soil moisture (Hamerlynck

and McAuliffe 2008). Understanding the short-term physiological responses of *Larrea*

and *Ambrosia* to increased summer rain pulses, especially as related to geomorphic

features that amplify a summer pulse, helps identify how plant communities may respond

to changes in the precipitation regime of the Mojave Desert; however, an analysis of canopy volume and reproductive output over repeated growing seasons would give insights about how these physiological responses translate into productivity and ultimately affect community dynamics.

CHAPTER 4

CONCLUSIONS AND BROADER IMPLICATIONS

These two studies have demonstrated how desert washes, which occupy only a small proportion of the spatial area of a bajada, have a pronounced effect on the structure and function of the co-dominant shrubs *Larrea* and *Ambrosia* in the Mojave Desert. LiDAR has proven to be a useful tool in determining how the presence of a railroad and paralleling road over the past 100+ years has influenced the natural hydrology of the landscape and impacted vegetation processes across large spatial scales. LiDAR introduces a certain amount of error when analyzing vegetation characteristics and spatial patterns of plants in desert ecosystems; however, this error can be accounted for by applying a correction function (linear regression) to derived plant heights. The minimum height for accurate LiDAR detection in this desert system was determined to be approx. 0.3 m. The inability of LiDAR to detect small shrubs such as *Ambrosia* presents a major limitation at this time because *Ambrosia* is an important component in the spatial arrangement of Mojave Desert shrubs, as it is co-dominant with *Larrea*. Despite these limitations, LiDAR has proven to be useful in characterizing spatial patterns of *Larrea* in relation to patterns of wash flow and disturbances that alter the natural hydrological regime. Using LiDAR we were able to identify where clustering occurred across the landscape, and when combined with field evidence, indicated that productivity of desert

shrubs is influenced by physical disturbances on the landscape (e.g., wash diversion), which ultimately can alter habitats and community dynamics in desert ecosystems.

Alternative energy projects and recreation in the Mojave Desert are placing increasing demands for more access roads, which ultimately impacts the hydrology across bajadas and the spatial distributions of plants. Long-term monitoring using LiDAR could provide a more comprehensive understanding of hydrology-driven productivity processes and the impacts of physical disturbances in deserts.

Changing climatic conditions, specifically the increase in intensity and frequency of summer rain events, may also have a pronounced effect on plant function, even in areas unaffected by physical disturbances. Significant changes in summer rainfall patterns, and thus increased wash flow, will affect the physiological responses of shrubs growing along wash margins, and subsequently could have an effect on overall plant fitness and survival. This small scale effect, both spatially and temporally, could in turn produce community level changes in plant structure.

Repeated photography and field observations show that plant populations and communities have changed over the past 100+ years in the Mojave Desert in response to climate variability such as prolonged drought or wet periods (Hereford et al. 2006). These changes could have resulted from fine-scale processes such as ephemeral pulses of summer water as demonstrated in this study, yet the majority of climate models are created at large temporal scales (e.g., annual or seasonal). Such models do not make predictions about the magnitude or variation of precipitation changes at smaller scales, the scale that is known to strongly influence plant and ecosystem responses to climate change (Weltzin et al. 2003). Therefore, research on smaller spatial (regional and local)

and temporal (days or months) scales, such as those used in this study, is crucial to improving long-term predictions about vegetation changes in response to altered climate patterns. A clearer understanding of how climate and landscape changes will alter ecosystem productivity of arid systems like the Mojave Desert will be greatly aided by improving our knowledge of the relationships between vegetation and physical properties of landscape, since, as demonstrated here, that landscape, and its disturbance, can have pronounced control on plant dispersion, physiological responses and production.

APPENDIX

CHARACTERIZATION OF SOILS AND ROOTS UNDER THE WASH

The wetted cross section area was about 2 m wide and 1 m deep; combined with the 30 m length of wetted wash, yielding a volume of 60 m^3 of wetted soil. The soil profile shown exhibits three basic layers of different age and origin. At the top is active wash sediment (A). It overlies alluvial fan sediment that is laterally continuous with adjacent surface Qya4 deposits (Bw). That fan sediment lies on older fan sediment with a second set of soils developed in it (2Bw).

Although the water infiltrated to the top of the basal calcic horizon that was well cemented, in detail the wetting front penetrated into the calcic horizon in an irregular geometry. Roots were not observed within the wash sediments (A) but were present throughout the underlying sediments (Bw, Bwk, 2Bw, 2Bwk1). In two places (28 and 51 cm depth), roots were concentrated in fine-textured beds or at boundaries between different soils. Particle size analysis through the section did not reveal large changes in texture, and all samples had little silt and clay.

Depth (cm)	Lithology	Soil Description	Roots (per 100 cm²)	Particle Size Analysis

% gravel

0   1   2   3   4

0   20   40   60

A - loose, poorly-sorted gravelly sand; *active wash*

(roots present at this level in cutbank)

Bw - orangish, thin bedded poorly-sorted gravelly sand with weak peds; *early Holocene alluvial fan*

1 woody

3 woody [many right at 28 cm depth]

Bwk - stage I to I+ calcic in thin bedded poorly-sorted gravelly sand

2Bw - orange with good peds; thin bedded poorly-sorted sand; *Pleistocene alluvial fan*

1 woody [many right at 51 cm depth]

2Bwk1 - stage I calcic in thin bedded poorly-sorted gravelly sand

2Bwk2 - stage II+ calcic cementing thin bedded poorly-sorted gravelly sand

0   2   4   6   8

% fines <125 μ

Depth markers: 0, 20, 40, 60, 80, 100

REFERENCES

Andersen HE, Reutebuch SE, McGaughey RJ (2006) A rigorous assessment of tree height measurements obtained using airborne LiDAR and conventional field methods. Canadian J of Remote Sens 32:355-366

Anderson DJ (1971) Pattern in desert perennials. J of Ecology 59:555-560

Atchley MC, de Soyza AG, Whitford WG (1999) Arroyo water storage and soil nutrients and their effects on gas-exchange of shrub species in the northern Chihuahuan Desert. J of Arid Environ 43:21-33

Balding FR, Cunningham GL (1974) The influence of soil water potential on the perennial vegetation of a desert arroyo. The Southwest Naturalist 19:241-248

Bamberg SA, Kleinkopf GE, Wallace A, Vollmer A (1975) Comparative photosynthetic production of Mojave Desert shrubs. Ecology 56:732-736

Barbour MG (1969) Age and space distribution of the desert shrub *Larrea divaricata*. Ecology 50:679-685

Barbour MG (1973) Desert dogma reexamined: root/shoot productivity and plant spacing. American Midl Naturalist 89:41-57

Barbour MG, Diaz DV (1973) *Larrea* plant communities on bajada and moisture gradients in the United States and Argentina. Vegetatio 28:335-352

Barbour MG, MacMahon JA, Bamberg SA, Ludwig JA (1977) The structure and distribution of *Larrea* communities. In: Mabry TJ, Hunziker JH, DiFeo Jr. DR (eds) Creosotebush: Biology and Chemistry of *Larrea* in New World Deserts. Dowden, Hutchinson & Ross, Inc. Stroudsburg Pennsylvania, pp 227-243

Barker DH, Vanier C, Naumberg E, Charlet TN, Nielsen KM, Newingham BA, Smith SD (2005) Enhanced monsoon precipitation and nitrogen deposition affect leaf traits and photosynthesis differently in spring and summer in the desert shrub *Larrea tridentata*. New Phytologist 169:799-808

BassiriRad H, Tremmel DC, Virginia RA, Reynolds JF, de Soyza AG, Brunell MH (1999) Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. Plant Ecology 145:27-36

Beatley JC (1974) Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856-863

Bedford DR (2003) Surficial and bedrock map database of the Kelso 7.5 minute quadrangle, San Bernardino County, California. U.S. Geological Survey Open-File Report No. 03-501. Denver, Colorado. http://geopubs.wr.usgs.gov/open-file/of03-501/

Bedford DR, Miller DM, Phelps GA (2006) Preliminary surficial geologic map database of the Amboy 30 x 60 minute quadrangle, California. U.S. Geological Survey Open-File Report No. 2006-1165. Denver, Colorado. http//pubs.usgs.gov/of/2006/1165/

Bedford DR, Miller DM, Schmidt KM, Phelps GA (2009) Landscape-scale relationships between surficial geology, soil texture, topography, and creosotebush size and density in the Eastern Mojave Desert of California. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, and Miller DM (eds.) The Mojave Desert: ecosystem processes and sustainability. University of Nevada Press, Reno, pp 252-277

Bolling JD, Walker LR (2000) Plant and soil recovery along a series of abandoned desert roads. J of Arid Environ 46:1-24

Brandtberg T, Warner T, Landenberger R, McGraw J (2003) Detection and analysis of individual leaf-off tree crowns in small-footprint, high sampling density LiDAR data from eastern deciduous forest in North America. Remote Sensing of Environ 85:290-303

Brisson J, Reynolds JF (1994) The effect of neighbors on root distribution in a creosotebush (*Larrea tridentata*) population. Ecology 75:1693-1702

Brooks ML, Lair BM (2009) Ecological effects of vehicular routes in a desert ecosystem. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, and Miller DM (eds.) The Mojave Desert: ecosystem processes and sustainability. University of Nevada Press, Reno, pp 168-195

Campbell GS, Harris GA (1981) Modeling soil-water-plant-atmosphere systems of deserts. In: Evans DD, Thames JL (eds) Water in Desert Ecosystems. Dowden, Hutchinson and Ross, Stroudsburg Pennsylvania, pp 75-91

Cannon WA (1911) The root habits of desert plants. Carnegie Institution of Washington, Washington, D.C.

Cannon WA (1913) Notes on root variation in some desert plants. The Plant World 16:323-341

Chew RM, Chew AE (1965) The primary productivity of a desert-shrub (*Larrea tridentata*) community. Ecological Monographs 35:355-375

Chou YH (1993) Critical issues in the evaluation of spatial autocorrelation. In: Frank AU, Campari I (eds.) Spatial information theory: A theoretical basis for GIS. Lecture Notes in Computer Science 716:421-433

Dixon PM (2002) Ripley's *K* function. In: El-Shaarawi AH, Piegorsch WW (eds) Encyclopedia of Envirometrics, vol. 3, John Wiley & Sons, Ltd, Chichester, pp 1796-1803

Dunnett CW (1955) A multiple comparison procedure for comparing several treatments with a control. J of the American Statistical Association 50:1096-1121

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TA, Mearns LO (2000) Climate extremes: Observations, modeling, and impacts. Science 289:2068-2074

Ebert TA, McMaster GS (1981) Regular pattern of desert shrubs: a sampling artifact? J of Ecology 69:559-564

Ehleringer JR, Cooper TA (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76:562-566

Ehleringer JR, Phillips SL, Schuster SF, Sandquist DR (1991) Differential utilization of summer rains by desert plants. Oecologia 88:430-434

Evans DD, Thames JL (1981) Desert hydrologic systems. In: Evans DD, Thames JL (eds) Water in desert ecosystems. Dowden, Hutchinson & Ross, Stroudsburg Pennsylvania, pp 265-272

Ezcurra E, Arizaga S, Valverde PL, Mourelle C, Flores-Martinez A (1992) Foliole movement and canopy architecture of *Larrea tridentata* (DC.) Cov. in Mexican deserts. Oecologia 92:83-89

Fonteyn PJ, Mahall BE (1981) An experimental analysis of structure in a desert plant community. J of Ecology 69:883-896

Franco AC, de Soyza AG, Virginia RA, Reynolds JF, Whitford WG (1994) Effects of plant size and water relations on gas exchange and growth of the desert shrub *Larrea tridentata*. Oecologia 97:171-178

Frank TD, Tweddale SA (2006) The effect of spatial resolution on measurement of vegetation cover in three Mojave Desert shrub communities. J of Arid Environ 67:88-99

Galiano EF (1982) Pattern detection in plant populations through the analysis of plant-to-all-plants distances. Vegetatio 49:39-43

Gaveau DLA, Hill RA (2003) Quantifying canopy height underestimation by laser pulse penetration in small-footprint airborne laser scanning data. Canadian J of Remote Sensing 29:650-657

Getis A, Ord JK (1992) The analysis of spatial association by use of distance statistics. Geographical Analysis 24:189-206

Getis A, Morrison AC, Gray K, Scott TW (2003) Characteristics of the spatial pattern of the dengue vector, *Aedes aegypti*, in Iquitos, Peru. The American J of Tropical Medicine and Hygiene 69:484-493

Gile LH, Gibbens RP, Lenz JM (1998) Soil-induced variability in root systems of creosotebush (*Larrea tridentata*) and tarbush (*Flourensia cernua*). J of Arid Environ 39:57-78

Griffiths PG, Hereford R, Webb RH (2006) Sediment yield and runoff frequency of small drainage basins in the Mojave Desert, U.S.A. Geomorphology 74:232-244

Habib A, Kersting AP, Bang KI, Lee DC (2010) Alternative methodologies for the internal quality control of parallel LiDAR strips. IEEE Transactions on Geoscience and Remote Sensing 48:221-236

Hamerlynck EP, McAuliffe JR, Smith SD (2000) Effects of surface and sub-surface soil horizons on the seasonal performance of *Larrea tridentata* (creosotebush). Functional Ecology 14:596-606

Hamerlynck EP, McAuliffe JR, McDonald EV, Smith SD (2002) Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. Ecology 83:768-779

Hamerlynck EP, McAuliffe JR (2008) Soil-dependent canopy-die back and plant mortality in two Mojave Desert shrubs. J of Arid Environ 72:1793-1802

Haase P (1995) Spatial pattern analysis in ecology based on Ripley's *K*-function: Introduction and methods of edge correction. J of Vegetation Science 6:575-582

Haase P, Pugnaire FI, Clark SC, Incoll LD (1996) Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain. J of Vegetation Science 7:527-534

Heckman, Jr. LH, Berkas WR (1981) Modeling desert runoff. In: Evans DD, Thames JL (eds) Water in desert ecosystems. Dowden, Hutchinson & Ross, Stroudsburg Pennsylvania, pp 244-264

Hereford R, Webb RH, Longpre CI (2006) Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893-2001. J of Arid Environ 67:13-34

Hillel D, Tadmor N (1962) Water regime and vegetation in the central Negev highlands of Israel. Ecology 43:33-41

Hollaus M, Wagner W, Eberhofer C, Karel W (2006) Accuracy of large-scale canopy heights derived from LiDAR data under operational constraints in a complex alpine environment. ISPRS J of Photogrammetry & Remote Sensing 60:323-338

Hopkinson C, Chasmer LE, Sass G, Creed IF, Sitar M, Kalbfleisch W, Treitz P (2005) Vegetation class dependent errors in LiDAR ground elevation and canopy height estimates in a boreal wetland environment. Canadian J of Remote Sensing 31:191-206

Johnson HB, Vasek FC, Yonkers T (1975) Productivity, diversity and stability relationships in Mojave Desert roadside vegetation. Bull of the Torrey Botanical Club 102:106-115

Jones CS (1984) The effect of axis splitting on xylem pressure potentials and water movement in the desert shrub *Ambrosia dumosa* (Gray) Payne (Asteraceae). Botanical Gaz 145:125-131

Karl TR, Knight RW (1997) Secular trends of precipitation amount, frequency and intensity in the United States. Bull of the American Meteorological Society 79:231-241

Karl TR, Melillo JM, Peterson TC (eds) (2009) Global climate change impacts in the United States. Cambridge University Press, New York

King TJ, Woodell SRJ (1973) The causes of regular pattern in desert perennials. J of Ecology 61:761-765

King TJ, Woodell SRJ (1984) Are regular patterns in desert shrubs artifacts of sampling. J of Ecology 72:295-298

Koukoulas S, Blackburn GA (2005) Spatial relationships between tree species and gap characteristics in broad-leaved deciduous woodland. J of Vegetation Science 16:587-596

Laffan SW (2006) Assessing regional scale weed distributions, with an Australian example using *Nassella trichotoma*. Weed Res 46:194-206

Lambers H, Chapin III FS, Pons TJ (2006) Plant Physiological Ecology, Springer Science + Business Media, New York

Law R, Illian J, Burslem DFRP, Gratzer G, Gunatilleke CVS, Gunatilleke IAUN (2009) Ecological information from spatial patterns of plants: insights from point process theory. J of Ecology 97:616-628

Lefsky MA, Cohen WB, Parker GG, Harding DJ (2002) LiDAR Remote Sensing for Ecosystem Studies. BioScience 52:19-30

Lightfoot DC, Whitford WG (1991) Productivity of creosotebush foliage and associated canopy arthropods along a desert roadside. American Midl Naturalist 125:310-322

Lin G, Phillips SL, Ehleringer JR (1996) Monsoonal precipitation responses in a cold desert community on the Colorado Plateau. Oecologia 106:8-17

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS® System for Mixed Models. SAS Institute Inc., Cary, NC

Ludwig JA, Whitford WG (1981) Short-term water and energy flow in arid ecosystems. In: Goodall DW, Perry RA (eds.) Arid-land ecosystems: structure, functioning and management. Cambridge University Press, New York, pp 271-300

MacMahon JA, Schimpf DJ (1981) Water as a factor in the biology of North American desert plants. In: Evans DD, Thames JL (eds) Water in Desert Ecosystems. Dowden, Hutchinson and Ross, Stroudsburg Pennsylvania, pp 92-113

Mahall BE, Callaway RM (1991) Root communication among desert shrubs. Proc of the Natl Academy of Sciences (USA) 88:874-876

McAuliffe, JR (1995) Landscape evolution, soil formation and Arizona's desert grasslands. In: McClaran MP, VanDevender TR (eds.) The Desert Grassland. University of Arizona Press, Tucson, pp 100-129

Miller DM, Bedford DR, Hughson DL, McDonald EV, Robinson SE, and Schmidt KM, (2009) Mapping Mojave Desert ecosystem properties with surficial geology. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, and Miller DM (eds.) The Mojave Desert: ecosystem processes and sustainability. University of Nevada Press, Reno, pp 225-251

Miller DM (2012) Surficial geologic map of the Ivanpah 30' x 60' quadrangle, San Bernardino County, California, and Clark County, Nevada. Scientific Investigations Map (SIM) http://pubs.usgs.gov/sim/3206/sim3206_pamphlet.pdf

Mitchell JJ, Glenn NF, Sankey TT, Derryberry DR, Anderson MO, Hruska RC (2011) Small-footprint LiDAR estimations of sagebrush canopy characteristics. Photogrammetric Engineering & Remote Sensing 77:521-530

Mooney HA, Bjorkman O, Collatz GJ (1978) Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata* I. Carbon dioxide exchange characteristics of intact leaves. Plant Physiology 61:406-410

Naumberg E, Housman DC, Huxman TE, Charlet TN, Loik ME, Smith SD (2003) Photosynthetic responses of Mojave Desert shrubs to free air CO_2 enrichment are greatest during wet years. Glob Change Biology 9:276-285

[NAST] National Assessment Synthesis Team (2000) Climate change impacts on the United States: The potential consequences of climate variability and change. US Global Change Research Program, Washington DC

Nimmo JR, Perkins KS, Schmidt KM, Miller DM, Stock JD, Singha K (2009) Hydrologic characterization of desert soils with varying degrees of pedogensis: 1. Field experiments evaluating plant-relevant soil water behavior. Vadose Zone J 8:480-495

Noy-Meir I (1973) Desert ecosystems: environment and producers. Annu Rev of Ecology & Systematics 4:25-41

Odening WR, Strain BR, Oechel WC (1974) The effect of decreasing water potential on net CO_2 exchange of intact desert shrubs. Ecology 55:1086-1095

Oechel WC, Strain BR, Odening WR (1972) Tissue water potential, photosynthesis, C-labeled photosynthate utilization, and growth in the desert shrub *Larrea divaricata* Cav. Ecological Monographs 42:127-141

Ogle K, Reynolds JF (2002) Desert dogma revisited: coupling of stomatal conductance and photosynthesis in the desert shrub, *Larrea tridentata*. Plant, Cell and Environ 25:909-921

Ogle K, Reynolds JF (2004) Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. Oecologia 141:282-294

Ogle K, Wolpert RL, Reynolds JF (2004) Reconstructing plant root area and water uptake profiles. Ecology 85:1967-1978

Ord JK, Getis A (1995) Local spatial autocorrelation statistics: distributional issues and an application. Geographical Analysis 27:286-306

O'Sullivan D, Unwin DJ (2003) Geographic Information Analysis. John Wiley & Sons, Inc., Hoboken, New Jersey

Pavlik BM (2008) The California deserts: An ecological rediscovery. University of California Press, Berkeley and Los Angeles, CA

Pelissier R, Goreaud F (2001) A practical approach to the study of spatial structure in simple cases of heterogeneous vegetation. J of Vegetation Science 12:99-108

Perry JN, Liebhold AM, Rosenberg MS, Dungan J, Miriti M, Jakomulska A, Pousty SC (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. Ecography 25:578-600

Peterson FF (1981) Landforms of the basin and range province defined for soil survey. Technical Bulletin No. 28. Nevada Agricultural Experiment Station, University of Nevada, Reno, Nevada

Phillips DL, MacMahon JA (1981) Competition and spacing patterns in desert shrubs. J of Ecology 69:97-115

Pielou EC (1960) A single mechanism to account for regular, random and aggregated populations. J of Ecology 48:575-584

Prentice IC, Werger MJA (1985) Clump spacing in a desert dwarf community. Vegetatio 63:133-139

Prose DV, Metzger SK, Wilshire HG (1987) Effects of substrate disturbance on secondary plant succession; Mojave Desert, California. J of Appl Ecology 24:305-313

Rango A, Chopping M, Ritchie J, Havstad K, Kustas W, Schmugge T (2000) Morphological characteristics of shrub coppice dunes in desert grasslands of southern New Mexico derived from scanning LiDAR. Remote Sensing of Environ 74:26-44

Reynolds JF, Kemp PR, Ogle K, Fernandez RJ (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141:194-210

Ripley BD (1977) Modeling spatial patterns. J of the Royal Statistical Society 39:172-212

Ronnholm P, Hyyppa J, Haggren H, Yu X, Kaartinen H (2004) Calibration of laser-derived tree canopy height estimates by means of photogrammetry techniques. Scandinavian J of For Res 19:524-528

Sankey TT, Bond P (2011) LiDAR-based classification of sagebrush community types. Rangel Ecology & Management 64:92-98 DOI 10.2111/REM-D-10-00019.1

Schenk HJ, Callaway RM, Mahall BE (1999) Spatial root segregation: Are plants territorial? Advances in Ecological Res 28:145-180

Schenk HJ, Holzapfel C, Hamilton JG, Mahall BE (2003) Spatial ecology of a small desert shrub on adjacent geological substrates. J of Ecology 91:383-395

Schlesinger WH, Jones CS (1984) The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. Botanical Gaz 145:116-124

Schlesinger WH, Fonteyn PJ, Reiners WA (1989) Effects of overland flow on plant water relations, erosion, and soil water percolation on a Mojave Desert landscape. Soil Science Society of America J 53:1567-1572

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. Science 247:1043-1048

Schwinning S, Ehleringer JR (2001) Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. J of Ecology 89:464-480

Schwinning S, Davis K, Richardson L, Ehleringer JR (2002) Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. Oecologia 130:345-355

Schwinning S, Starr BI, Ehleringer JR (2003) Dominant cold desert plants do not partition warm season precipitation by event size. Oecologia 136:252-260

Schwinning S, Hooten MM (2009) Mojave Desert root systems. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, and Miller DM (eds.) The Mojave Desert: ecosystem processes and sustainability. University of Nevada Press, Reno, pp 278-311

Schwinning S, Sandquist DR, Miller DM, Bedford DR, Phillips SL, Belnap J (2011) The influence of stream channels on distributions of *Larrea tridentata* and *Ambrosia dumosa* in the Mojave Desert, CA, USA: patterns, mechanisms and effects on stream redistribution. Ecohydrology 4:12-25

Schmitt AK, Martin CE, Loeschen VS, Schmitt A (1993) Mid-summer gas exchange and water relations of seven C_3 species in a desert wash in Baja California, Mexico. J of Arid Environ 24:155-164

Singh SP (1978) Root-shoot habit of *Larrea divaricata Cav.* Transactions of the Kansas Academy of Science 81:243-249

Skarpe, C (1991) Spatial patterns and dynamics of woody vegetation in an arid savanna. J of Vegetation Science 2:565-572

Smith SD, Herr CA, Leary KL, Piorkowski JM (1995) Soil-plant water relations in a Mojave Desert mixed shrub community: a comparison of three geomorphic surfaces. J of Arid Environ 29:339-351

Smith SD, Monson RK, Anderson JE (1997) Physiological Ecology of North American Desert Plants. Springer-Verlag, Berlin Germany

Snyder KA, Donovan LA, James JJ, Tiller RL, Richards JH (2004) Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. Oecologia 141:325-334

Sokal RR (1998) Local spatial autocorrelation in biological variables. Biological J of the Linnean Society 65:41-62

Stock JD, Schmidt KM, Miller DM (2008) Controls on alluvial fan long-profiles. Geological Society of America Bull 120:619-640 DOI 10.1130/B26208.1

Streutker DR, Glenn NF (2006) LiDAR measurement of sagebrush steppe vegetation heights. Remote Sensing of the Environ 102:135-145

Su JG, Bork EW (2007) Characterization of diverse plant communities in Aspen Parkland rangeland using LiDAR data. Appl Vegetation Science 10:407-416

Thames JL, Evans DD (1981) Desert systems: An overview. In: Evans DD, Thames JL (eds) Water in desert ecosystems. Dowden, Hutchinson & Ross, Stroudsburg Pennsylvania, pp 1-12

Thomas V, Treitz P, McCaughey JH, Morrison I (2006) Mapping stand-level forest biophysical variables for a mixedwood boreal forest using LiDAR: an examination of scanning density. Canadian J of For Res 36:34-47

Thornbury WD (1969) Principles of Geomorphology. John Wiley & Sons, Inc., New York

Tietjen B, Zehe E, Jeltsch F (2009) Simulating plant water availability in dry lands under climate change: A generic model of two soil layers. Water Resources Res 45: 1-14

Tirado R, Pugnaire FI (2003) Shrub spatial aggregation and consequences for reproductive success. Oecologia 136:296-301

Vasek FC (1980) Creosote Bush: Long-lived clones in the Mojave Desert. American J of Botany 67:246-255

Wallace A, Romney EM (1972) Radioecology and ecophysiology of desert plants at the Nevada test site. U.S. Atomic Energy Commission, Washington, D.C.

Walter H (1963) The water supply of desert plants. In: Rutter AJ, Whitehead FH (eds.) The water relations of plants. John Wiley & Sons, New York, pp 278-311

Wang C, Glenn NF (2008) A linear regression method for tree canopy height estimation using airborne LiDAR data. Canadian J of Remote Sensing 34:S217-S227

Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin G, Pockman, WT, Shaw R, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. BioScience 53:941-952

Wiegand T, Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104:209-229

Wilcox CS, Ferguson JW, Fernandez GCJ, Nowak RS (2004) Fine root growth dynamics of four Mojave Desert shrubs as related to soil moisture and microsite. J of Arid Environ 56:129-148

Woodell SRJ, Mooney HA, Hill AJ (1969) The behaviour of *Larrea divaricata* (creosote bush) in response to rainfall in California. J of Ecology 57:37-44

Yan S, Wan C, Sosebee RE, Wester DB, Fish EB, Zartman RE (2000) Responses of photosynthesis and water relations to rainfall in the desert shrub creosote bush (*Larrea tridentata*) as influenced by municipal biosolids. J of Arid Environ 46:397-412

Yoder CK, Nowak RS (1999) Soil moisture extraction by evergreen and drought-deciduous shrubs in the Mojave Desert during wet and dry years. J of Arid Environ 42:81-96